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# A model of oxygen uptake kinetics in response to exercise: Including a means of calculating oxygen demand/deficit/debt

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## Abstract

We present a new model of the underlying dynamics of the oxygen uptake  $\dot{V}O_2(v, t)$  kinetics for various exercise intensities. This model is in the form of a set of nonlinear coupled vector fields for the  $\dot{V}O_2(v, t)$  and  $\dot{v}$ , the derivative of the exercise intensity with respect to time. We also present a new and novel means for calculating the oxygen demand,  $D(v, t)$ , and hence also the oxygen deficit and debt, given the time series of the  $\dot{V}O_2(v, t)$ . This enables us to give better predictions for these values especially for when exercising at or close to maximal exercise intensities. Our model also allows us to predict the oxygen uptake time series given the time series for the exercise intensity as well as to investigate the oxygen uptake response to nonlinear exercise intensities. Neither of these features is possible using the currently used three-phase model. We also present a review of both the underlying physiology and the three-phase model. This includes for the first time a complete set of the analytical solutions of the three-phase model for the oxygen deficit and debt.

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## 1. Introduction: general

An understanding of the oxygen uptake kinetics is fundamental to training methodology and competitive success in sport (Martin and Coe, 1997; Noakes, 2003; Astrand et al., 2003; Billat, 2001a,b; Saltin et al., 1995b,a; Bangsbo et al., 2000) and also to our knowledge of cardiovascular health (Wasserman et al., 1999). A correct and efficient means of interpreting and analyzing the data obtained is of vast importance, as exercise testing is routinely used in both of these areas. The currently used model of the oxygen uptake kinetics is the three-phase model (Davies et al., 1972; Whipp and Wasserman, 1972; Linnarsson, 1974; Barstow and Mole, 1991). In the introductions we review and present some of the problems and difficulties with this model (see also Stirling and Zakyntinaki (submitted for publication)) as well as for the first time a complete set of analytical solutions for the oxygen deficit and debt. We then go onto present our model which uses tools from dynamical systems (see Kantz and Schreiber, 1999; Guckenheimer and Holmes, 1983) to model the underlying dynamics or basic response pattern of the time series of the oxygen uptake kinetics. This new model contrasts the three-phase model in as much as it consists of a smooth function of both time and exercise intensity and therefore does not contain any phases or time delays. The new model allows us to provide more accurate estimations of the oxygen demand over the continuum of exercise intensities and as a result better estimations of the oxygen deficit and debt. Other main advantages of this new model are that it gives one the possibility of studying the response to nonlinear exercise intensities and also of making predictions of the time series of the oxygen uptake kinetics given the time series of the exercise intensity. Neither of these two advantages was previously available using the three-phase model.

### 1.1. The three-phase model for pulmonary $\dot{V}O_2$ , the critical speed, $v_{\text{crit}}$ , and the $\dot{V}O_2$ drift

Hill and Lupton (1923) recognized that the pulmonary  $\dot{V}O_2$  rises approximately exponentially following the onset of moderate exercise. With breath-by-breath analysis however, three phases are believed to be observable in the  $\dot{V}O_2(t)$  time series. Phase 1 occurs in the first 10 to 25 s, with the rise in  $\dot{V}O_2$  believed to be due primarily to increased cardiac output (Wasserman et al., 1974) and secondarily to changes in mixed venous  $O_2$  content (Casaburi et al., 1989b) and lung gas stores (Barstow and Mole, 1987). Phase 2 follows phase 1, and in this phase there is an fast exponential-like rise to a steady-state level of  $\dot{V}O_2$  for moderate exercise below the lactate threshold, LT (Casaburi et al., 1989a; Whipp and Wasserman, 1972; Barstow, 1994). The so-called lactate threshold, LT, is defined as the point at which blood lactate begins to accumulate, above resting levels during exercise of increasing intensity (Weltman, 1995). Phase 3 represents the new steady-state level of  $\dot{V}O_2$ , when it is achieved (i.e. below LT). Below the LT,  $\dot{V}O_2$  reaches a steady state within approximately 3 min of constant work rate exercise (Davies et al., 1972; Linnarsson, 1974; Whipp and Wasserman, 1972). At higher rates of work however the  $\dot{V}O_2(t)$  does not follow the steady-state response. Instead at work rates above the lactate threshold the oxygen consumption continues to increase beyond the typical time for reaching the steady-state value. This slow increase in  $\dot{V}O_2$  during constant work rate exercise has been called the slow component of oxygen uptake kinetics and is commonly

believed (Barstow and Mole, 1991), though not universally, (see Linnarsson, 1974; MacDonald et al., 1997, where phases 2 and 3 start together) believed to start 100 to 200 s into the exercise. The slow component can result in either a delayed sub-maximal steady state or a steady state equal to the  $\dot{V}O_{2\max}$  (Billat et al., 2000). It has been described as an additional phase in which  $\dot{V}O_2$  adds on top of the metabolic requirements of that work rate (Paterson and Whipp, 1991). There has also been much debate as to the cause of the slow component. Gaesser and Poole (1996) in their review article conclude that “although the blood lactate profile is well correlated with the time course and magnitude of the slow component the relationship is coincidental rather than causal. The most likely mechanism accounting for the slow component is muscle fibre recruitment”; see also Poole (1994) and Poole et al. (1994).

Billat (2000) defines the critical speed,  $v_{\text{crit}}$ , to be the highest speed for which the  $\dot{V}O_2$  can reach a delayed (due to the slow component), sub-maximal steady state. Likewise Hill and Ferguson (1999) demonstrated that “the  $v_{\text{crit}}$  is the threshold intensity above which exercise of sufficient duration will lead to the attainment of  $\dot{V}O_{2\max}$ ”. This is used (Hill et al., 2002) to define the lower boundary for severe exercise as “just above  $v_{\text{crit}}$ , which is the highest work rate that is sustainable for a prolonged duration and that will not elicit  $\dot{V}O_{2\max}$ ”.

The  $\dot{V}O_2$  slow component should not be confused with a phenomenon called the  $\dot{V}O_2$  drift. This phenomenon is defined as a slow increase in  $\dot{V}O_2$  during prolonged, sub-maximal, constant power output exercise (Coyle et al., 1991; Hamilton et al., 1991; Kalis et al., 1988). Unlike the slow component, the  $\dot{V}O_2$  drift is observed at power outputs well below lactate threshold and the magnitude of the increase in  $\dot{V}O_2$  is much less (Gaesser and Poole, 1996).

### 1.2. *Fluctuations in $\dot{V}O_2$ , averaging over repeated runs and phases*

Linnarsson (1974) states that “Respiratory and circulatory functions exhibit spontaneous fluctuations which will be superimposed as a ‘noise’ on the basic response pattern during the adaption to exercise, and become noticeable when breath-by-breath or beat-by-beat recordings are made”. Such oscillations or fluctuations can be a result of noise due to the measuring device or can be physiological, such as abnormal breathing during exercise including shallow breathing or breath holding (Borroni et al., 2001). Regarding the significance of this noise, Borroni et al. (2001) state “it is not possible to exclude the fact that the breath-by-breath variability may have biological significance, although Lamarra et al. (1987), suggest stochastic properties of the breath-by-breath noise” (see also Potter et al., 1999; Puente-Maestu et al., 2002; Xing et al., 1991; Rossiter et al., 2000; Koga, 1990; Borroni et al., 2001). There is also a potential biological significance of breath-by-breath interbreath fluctuations in exercise situations in which the breathing pattern is altered, as is the case in swimming (Rodríguez et al., 2003) due to the cyclic head immersion and the resulting breath holding phase. Nonlinear systems such as the physiological ones in question however can produce signals which look noisy (Kantz and Schreiber, 1999; Guckenheimer and Holmes, 1983). As a result, part of what is attributed to noise could contain an inherent feature of the system being studied and need not necessarily be completely random.

The time series for the  $\dot{V}O_2$  is usually averaged before the data is modelled. For example Linnarsson (1974) states that “In order to reduce this noise and correspondingly enhance the basic response pattern, repeated identical experiments were averaged, both for individual and for the whole group of subjects”. This is used extensively in the work on modelling of the oxygen uptake or heart rate kinetics particularly when focusing on modelling a phase which is of short time duration, such as phase 2 in these models (Barstow and Mole, 1991; Linnarsson, 1974; Lamarra et al., 1987). It is after this averaging that one is able to see the features that are termed the three phases. In particular the time delay for the third phase can only be seen clearly after such averaging, as before the averaging there exist too many oscillations in the signal to identify the separate phases. Some other works which model the same general phenomena but focus more on a phase which lasts for a longer duration (i.e. the slow component) have however used only a single transition as they were able to obtain enough data to fit the parameters in their model (Borrani et al., 2001; Bearden and Moffatt, 2000; Bernard et al., 1998; Langsetmo and Poole, 1999; Langsetmo et al., 1997; Obert et al., 2000). In Bearden and Moffatt (2000) this data was then averaged using a rolling three-breath average before a three-phase model was fitted, whilst in Borrani et al. (2001) the data was edited with the points considered to be outliers removed and then the three-phase model was fitted. In both of these cases however due to the spread of the data it is not obvious that three phases are needed in the model or secondly that there exist different time delays for the second and third phases (see in particular Borrani et al., 2001). Both models (Borrani et al., 2001; Bearden and Moffatt, 2000) include these features however as they claim that the particular exponentials used for curve fitting fit better statistically with a time delay. The improvement in fit following the introduction of a time delay is marginal however and, bearing in mind that only a specific family of exponentials were used to model real noise-containing data, the existence of time delays in the time series of a single bout of exercise is highly debatable.

We argue that a more rigorous and useful way to remove the so-called noise and hence obtain the underlying signal is to remove the high frequency oscillations from the time series for a single bout of exercise using Fourier analysis and then reconstruct the smooth curve using the inverse Fourier transform. This is discussed in Zakyntinaki and Stirling (submitted for publication) and Stirling and Zakyntinaki (submitted for publication) in which this technique is applied to a very similar type of time series obtained for the heart rate response to exercise.

### 1.3. $O_2$ demand, deficit and debt

Oxygen demand,  $D(v, t)$ , is traditionally thought to be a constant equal to the end of exercise steady state  $\dot{V}O_{2ss}$ . This value is a function of speed (or intensity) such that an increase in the intensity of the exercise results in an increased oxygen demand. However the assumption that the demand is constant throughout constant speed exercise is based on the assumption that the energy demand does not increase with time when exercising at a constant speed. This assumption would not hold if the body was to become less efficient as time progresses, resulting in an increase in the amount of energy required to hold a particular speed. This would be particularly noticeable for exercises of a sufficiently high intensity. For exercises of a sufficiently low intensity however it could well be a good

approximation to assume that the oxygen demand is constant. We therefore believe the oxygen demand to be a function of both speed and time over the continuum of exercise intensities. The traditional view of the oxygen demand has also been challenged elsewhere (Bearden and Moffatt, 2000; Paterson and Whipp, 1991; Ren et al., 1989). The latter authors believe there to be an additional  $O_2$  demand beginning some time after the onset of exercise for work rates above the lactate threshold, in the same manner as the way Paterson and Whipp (1991) conceive the slow component to be an additional metabolic demand on top of that of the work rate requirements. Whether this is the case or not is debatable however. Borrani et al. (2001) point out that due to the difficulty in evaluating the energy demands “it seems very difficult to verify whether the slow component amplitude represents  $O_2$  excess or not”.

The oxygen deficit,  $O_2^{\text{defi}}$ , was defined as the integral with respect to time of the difference between the oxygen demand and the oxygen uptake during an exercise bout (Krogh and Lindhard, 1920). In the same paper (Krogh and Lindhard, 1920) the authors compared the oxygen deficit with another quantity called the oxygen debt,  $O_2^{\text{debt}}$ , to investigate how the oxygen deficit accumulated during exercise was repaid in recovery. The oxygen debt,  $O_2^{\text{debt}}$ , was defined as the volume of oxygen consumed above basal, resting values during recovery (Krogh and Lindhard, 1920; Meyerhof, 1920). The oxygen debt has also been called the Philogislon debt (Harris, 1969), recovery  $O_2$  (Stainsby and Barclay, 1970) and more recently excess post-exercise oxygen consumption (Brooks et al., 1971; Brooks and Gaesser, 1980; Gaesser and Brooks, 1984). In this paper however we will use the term oxygen debt. The oxygen deficit is often used to quantify the anaerobic energy contribution to the work performed. Energy costs or oxygen demands must be accurately known for calculating the oxygen deficit. This is not difficult at sub-maximal work loads where the steady-state oxygen uptake represents the oxygen demand. For exhaustive exercise, however, the nature of the true cost is more complicated, the problem being that we cannot extrapolate from the sub-maximal linear relationship as this would underestimate the oxygen deficit (Saltin, 1987, 1990; Bangsbo, 1996a,b, 1998). We also cannot assume that the mechanical efficiency of the subject remains constant with increasing intensity. It can be shown that the higher the intensity of the exercise the lower the mechanical efficiency of the athlete (Saltin et al., 1972; Saltin, 1987, 1990; Bangsbo, 1996a). A problem can also arise if, for what ever reason, the athlete stops exercising before a steady state is achieved as we would not know the  $\dot{V}O_{2\text{ss}}$  and hence the demand.

It has also been observed that if the athlete is sufficiently motivated then the same oxygen deficit is achieved when the tolerable exercise duration (i.e. the duration of time elapsed before the athlete stops due to exhaustion) ranges from 2 to 16 min (Astrand and Saltin, 1961; Karlsson and Saltin, 1970; Medbo et al., 1988). From the tolerable duration this appears to be in a range of intensities above the critical speed (Billat, 2001a). This indicates that when the  $D(v, t) > \dot{V}O_{2\text{max}}$  and the athlete runs until exhaustion then the deficit will not increase with intensity and, hence, will be no greater than the maximum oxygen deficit,  $O_{2\text{max}}^{\text{defi}}$ .

Bearden and Moffatt (2000) (see also Whipp et al., 2002; Kindig et al., 2001; Barstow et al., 1993) consider the oxygen deficit to consist of two components, due to their use of the three-phase model to model  $\dot{V}O_2$  kinetics above the lactate threshold (note that they also state however that this is “almost certainly an oversimplification of the complex

kinetics . . .”). The two separate components correspond to oxygen deficits for the so-called fast (phase 2) and slow (phase 3) components of oxygen uptake kinetics.

The new model that we propose can also be applied to the estimation of  $\dot{V}O_2$  values during exercise from measurements during the immediate recovery period by backwards extrapolation as proposed by Montpetit et al. (1981), and used by Costill et al. (1985) and others or, more recently, by breath-by-breath measurements (Rodriguez, 2000). Our model could also have important applications in computer simulation models of metabolism during exercise (Mader, 2003; Rodriguez and Mader, 2003).

**2. Introduction: theoretical**

First we introduce and review the mathematical details of the currently used three-phase model. We then go on to show how it can be used to generate solutions for the oxygen deficit and debt. We give for the first time complete solutions including the contributions from all three phases and show how they can be simplified. Solutions which have already appeared in the literature are acknowledged where appropriate.

*2.1. The three-phase model*

The  $\dot{V}O_2$  uptake kinetics for the on-transient is commonly modelled using the following double-exponential form (Barstow, 1994):

$$\begin{aligned} \dot{V}O_2 = & \dot{V}O_2(0) + A_0^{on} \left( 1 - e^{-\frac{t}{\tau_0^{on}}} \right) \quad \text{phase 1} \\ & + A_1^{on} \left( 1 - e^{-\frac{(t-TD_1^{on})}{\tau_1^{on}}} \right) \quad \text{phase 2} \\ & + A_2^{on} \left( 1 - e^{-\frac{(t-TD_2^{on})}{\tau_2^{on}}} \right) \quad \text{slow component} \end{aligned} \tag{1}$$

where  $\dot{V}O_2(0)$  is the initial value of the  $\dot{V}O_2$  at time  $t = 0$ .  $A_0^{on}$ ,  $A_1^{on}$  and  $A_2^{on}$  are the asymptotic values,  $\tau_0^{on}$ ,  $\tau_1^{on}$  and  $\tau_2^{on}$  are the time constants, and  $TD_1^{on}$  and  $TD_2^{on}$  are time delays for each exponential term; see Fig. 1. We define

$$\begin{aligned} A_{0_n}^{on} = & A_0^{on} \left( 1 - e^{-\frac{-TD_1^{on}}{\tau_0^{on}}} \right), & A_{1_n}^{on} = & A_1^{on} \left( 1 - e^{-\frac{-(TD_2^{on}-TD_1^{on})}{\tau_1^{on}}} \right) \\ \text{and } A_{2_n}^{on} = & A_2^{on} \left( 1 - e^{-\frac{-(t_f-TD_2^{on})}{\tau_2^{on}}} \right). \end{aligned}$$

The three-phase model is such that after  $t = TD_1^{on}$  we terminate phase 1 and put  $\dot{V}O_2(TD_1^{on}) = \dot{V}O_2(0) + A_{0_n}^{on}$ ; the second phase then starts and is added to  $\dot{V}O_2(TD_1^{on})$ . Phase 2 is terminated after  $t = TD_2^{on}$ , giving  $\dot{V}O_2(TD_2^{on}) = \dot{V}O_2(0) + A_{0_n}^{on} + A_{1_n}^{on}$ ; the third phase then starts and is added to  $\dot{V}O_2(TD_2^{on})$ . Phase 3 is terminated after  $t = t_f$  giving  $\dot{V}O_2(t_f) = \dot{V}O_2(0) + A_{0_n}^{on} + A_{1_n}^{on} + A_{2_n}^{on}$ . Note that below the so-called LT there is no slow

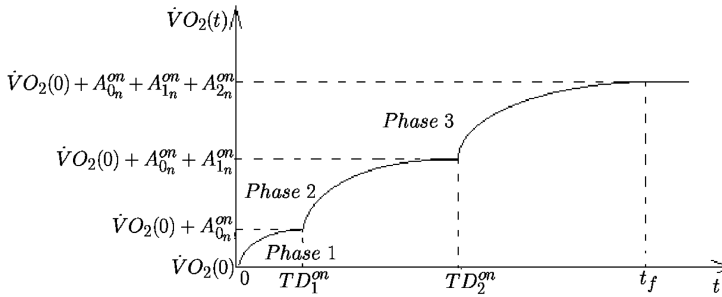


Fig. 1. The three-phase model for the on-transient kinetics of oxygen uptake.

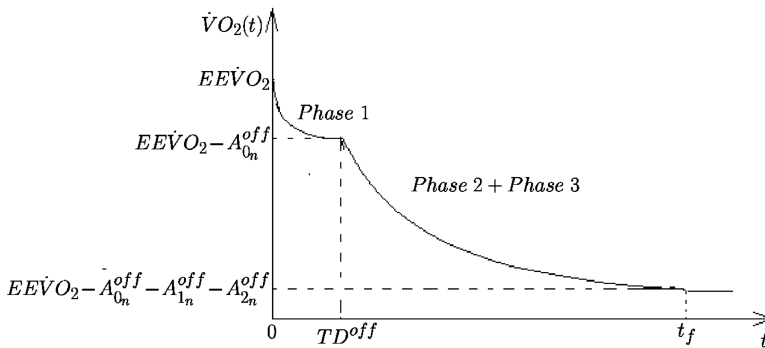


Fig. 2. The three-phase model for the off-transient oxygen uptake kinetics.

component or phase 3 and hence the model will have only two phases. Note also that when phase 1 is active, phase 2 and the slow component are inactive due to the time delays  $TD_1^{on}$  and  $TD_2^{on}$  respectively. Phase 2 becomes active after  $t = TD_1^{on}$ , which is approximately 10 s, followed by the slow component after  $t = TD_2^{on}$ , which is approximately 180 s.

It should also be noted that many models have  $A_0^{on} = 0$  as this initial cardiodynamic phase of the  $\dot{V}O_2$  response (phase 1) does not directly represent active muscle  $O_2$  utilization (Krogh and Lindhard, 1913; Weissman et al., 1982); hence the first 20 s of the on phase is often omitted from the curve fitting process (Ozyener et al., 2001). Also some models also have a common time delay such as  $TD^{on} = TD_1^{on} = TD_2^{on}$  as it is not necessarily proven physiologically that the slow component should really start after a different time delay than that of phase 2 (MacDonald et al., 1997; Linnarsson, 1974).

The off-transient kinetics (see Fig. 2) is modelled (Engelen et al., 1996) using the following form:

$$\dot{V}O_2 = EE\dot{V}O_2 - A_0^{off} \left( 1 - e^{-\frac{t}{\tau_0^{off}}} \right) - A_1^{off} \left( 1 - e^{-\frac{(t-TD^{off})}{\tau_1^{off}}} \right)$$

$$- A_2^{\text{off}} \left( 1 - e^{-\frac{(t-TD_1^{\text{off}})}{\tau_2^{\text{off}}}} \right) \tag{2}$$

where the parameters are as before apart from the fact that the superscript ‘on’ is replaced by ‘off’ to show that the parameters now refer to the off-transient kinetics. The parameter  $EE\dot{V}O_2$  is the end-exercise level of  $\dot{V}O_2$  and the time delay  $TD_1^{\text{off}} = TD_2^{\text{off}} = TD^{\text{off}}$ , as the phase 2 dynamics and the slow component begin at different times during the intense exercise, but in the off phase they exist together at the time at which the off phase begins. In Engelen et al. (1996) phase 1 was believed to be present in both the on and off responses to exercise; however, other authors (Ozyener et al., 2001; Bearden and Moffatt, 2000; Billat et al., 2002) do not include a first phase, and hence they have  $A_0^{\text{off}} = 0$ . As in the case of the on-transient we define

$$A_{0_n}^{\text{off}} = A_0^{\text{off}} \left( 1 - e^{-\frac{-TD^{\text{off}}}{\tau_0^{\text{off}}}} \right), \quad A_{1_n}^{\text{off}} = A_1^{\text{off}} \left( 1 - e^{-\frac{-(t_f-TD^{\text{off}})}{\tau_1^{\text{off}}}} \right)$$

$$\text{and } A_{2_n}^{\text{off}} = A_2^{\text{off}} \left( 1 - e^{-\frac{-(t_f-TD^{\text{off}})}{\tau_2^{\text{off}}}} \right)$$

whilst taking into account that the phase 2 and 3 have a common time delay,  $TD^{\text{off}}$ .

2.2. Oxygen deficit and debt solutions

The oxygen deficit is defined (Bearden and Moffatt, 2000) in two ways from Eq. (2). The first way is the traditional way where the oxygen deficit,  $O_{2_{\text{trad}}}^{\text{defi}}$ , is the difference between the oxygen that would have been consumed if the steady state,  $\dot{V}O_{2_{\text{ss}}}$ , had occurred from  $t = 0$  and the actual oxygen consumed,  $\dot{V}O_2(t)$ . The second way consists of using two separate oxygen deficits for the two separate oxygen demands of the phases 1 and 2. This is because as was discussed in Section 1.3 they considered the slow component to be an excess oxygen demand above the metabolic demands of the exercise intensity.

Below we give the analytical solutions for each case including all three phases; we then simplify the solutions to show the form of the equations under certain assumptions.

$$O_{2_{\text{trad}}}^{\text{defi}} = (\dot{V}O_2(0) + A_{0_n}^{\text{on}} + A_{1_n}^{\text{on}} + A_{2_n}^{\text{on}})(t_f - t_0) - \int_{t_0=0}^{t_f} \dot{V}O_2 dt \tag{3}$$

$$O_{2_{b\&m}}^{\text{defi}} = (\dot{V}O_2(0) + A_{0_n}^{\text{on}} + A_{1_n}^{\text{on}} + A_{2_n}^{\text{on}})(t_f - t_0) - (A_{2_n}^{\text{on}}TD_2^{\text{on}}) - \int_{t_0=0}^{t_f} \dot{V}O_2 dt \tag{4}$$

where

$$\int_{t_0=0}^{t_f} \dot{V}O_2 dt = \dot{V}O_2(0)t_f$$

$$+ A_{0_n}^{\text{on}}(t_f - TD_1^{\text{on}}) + A_{1_n}^{\text{on}}(t_f - TD_2^{\text{on}})$$

$$+ \int_{t_0=0}^{TD_1^{\text{on}}} A_0^{\text{on}} \left( 1 - e^{-\frac{t}{\tau_0^{\text{on}}}} \right) dt$$

$$\begin{aligned}
 & + \int_{TD_1^{\text{on}}}^{TD_2^{\text{on}}} A_1^{\text{on}} \left( 1 - e^{-\frac{(t-TD_1^{\text{on}})}{\tau_1^{\text{on}}}} \right) dt \\
 & + \int_{TD_2^{\text{on}}}^{t_f} A_2^{\text{on}} \left( 1 - e^{-\frac{(t-TD_2^{\text{on}})}{\tau_2^{\text{on}}}} \right) dt.
 \end{aligned} \tag{5}$$

Substituting Eq. (5) into Eqs. (3) and (4) we obtain

$$\begin{aligned}
 O_{2\text{trad}}^{\text{defi}} & = -A_0^{\text{on}} TD_1^{\text{on}} e^{-\frac{TD_1^{\text{on}}}{\tau_0^{\text{on}}}} \\
 & + A_1^{\text{on}} \left( TD_1^{\text{on}} - TD_2^{\text{on}} e^{-\frac{TD_2^{\text{on}}-TD_1^{\text{on}}}{\tau_1^{\text{on}}}} \right) \\
 & + A_2^{\text{on}} \left( TD_2^{\text{on}} - t_f e^{-\frac{t_f-TD_2^{\text{on}}}{\tau_2^{\text{on}}}} \right) \\
 & - A_0^{\text{on}} \tau_0^{\text{on}} \left( e^{-\frac{TD_1^{\text{on}}}{\tau_0^{\text{on}}}} - 1 \right) \\
 & - A_1^{\text{on}} \tau_1^{\text{on}} \left( e^{-\frac{TD_2^{\text{on}}-TD_1^{\text{on}}}{\tau_1^{\text{on}}}} - 1 \right) \\
 & - A_2^{\text{on}} \tau_2^{\text{on}} \left( e^{-\frac{t_f-TD_2^{\text{on}}}{\tau_2^{\text{on}}}} - 1 \right).
 \end{aligned} \tag{6}$$

$$\begin{aligned}
 O_{2b\& m}^{\text{defi}} & = -A_0^{\text{on}} TD_1^{\text{on}} e^{-\frac{TD_1^{\text{on}}}{\tau_0^{\text{on}}}} \\
 & + A_1^{\text{on}} \left( TD_1^{\text{on}} - TD_2^{\text{on}} e^{-\frac{TD_2^{\text{on}}-TD_1^{\text{on}}}{\tau_1^{\text{on}}}} \right) \\
 & + A_2^{\text{on}} (TD_2^{\text{on}} - t_f) e^{-\frac{t_f-TD_2^{\text{on}}}{\tau_2^{\text{on}}}} \\
 & - A_0^{\text{on}} \tau_0^{\text{on}} \left( e^{-\frac{TD_1^{\text{on}}}{\tau_0^{\text{on}}}} - 1 \right) \\
 & - A_1^{\text{on}} \tau_1^{\text{on}} \left( e^{-\frac{TD_2^{\text{on}}-TD_1^{\text{on}}}{\tau_1^{\text{on}}}} - 1 \right) \\
 & - A_2^{\text{on}} \tau_2^{\text{on}} \left( e^{-\frac{t_f-TD_2^{\text{on}}}{\tau_2^{\text{on}}}} - 1 \right).
 \end{aligned} \tag{7}$$

If we look at solutions where we assume that we have neither the first nor the third phase, then we have  $A_0^{\text{on}} = A_2^{\text{on}} = TD_1^{\text{on}} = TD_2^{\text{on}} = 0$  which gives  $O_2^{\text{defi}} = A_1^{\text{on}} \tau_1^{\text{on}} \left( 1 - e^{-\frac{t_f}{\tau_1^{\text{on}}}} \right)$  which when taken in the limit where  $t_f$  approaches infinity gives  $O_2^{\text{defi}} = A_1^{\text{on}} \tau_1^{\text{on}}$ . Such

solutions where there is no slow component work for intensities below the so-called lactate threshold (Whipp, 1994). We now remove the first 20 s from the data as is commonly done and set  $A_0^{on} = 0$  as in Bearden and Moffatt (2000). We also let  $t_0 = TD_1^{on} = 0$  as phase 1 has been removed; hence

$$\begin{aligned}
 O_{2_{trad}}^{defi} &= -A_1^{on}TD_2^{on}e^{-\frac{TD_2^{on}}{\tau_1^{on}}} \\
 &+ A_2^{on}\left(TD_2^{on} - t_f e^{-\frac{t_f - TD_2^{on}}{\tau_2^{on}}}\right) \\
 &- A_1^{on}\tau_1^{on}\left(e^{-\frac{TD_2^{on}}{\tau_1^{on}}} - 1\right) \\
 &- A_2^{on}\tau_2^{on}\left(e^{-\frac{t_f - TD_2^{on}}{\tau_2^{on}}} - 1\right). \tag{8}
 \end{aligned}$$

$$\begin{aligned}
 O_{2_{b\&m}}^{defi} &= -A_1^{on}TD_2^{on}e^{-\frac{TD_2^{on}}{\tau_1^{on}}} \\
 &+ A_2^{on}(TD_2^{on} - t_f)e^{-\frac{t_f - TD_2^{on}}{\tau_2^{on}}} \\
 &- A_1^{on}\tau_1^{on}\left(e^{-\frac{TD_2^{on}}{\tau_1^{on}}} - 1\right) \\
 &- A_2^{on}\tau_2^{on}\left(e^{-\frac{t_f - TD_2^{on}}{\tau_2^{on}}} - 1\right). \tag{9}
 \end{aligned}$$

We now make the assumption that there is also a common time delay starting after phase 1 such that  $TD^{on} = TD_1^{on} = TD_2^{on}$ . If we also assume that  $t_0 = TD^{on} = 0$  as we have removed the first phase from the data then we have, using the traditional definition and taking into account the new limits for the integrals in Eq. (5),

$$\begin{aligned}
 O_{2_{trad}}^{defi} &= -A_1^{on}t_f e^{-\frac{t_f}{\tau_1^{on}}} - A_2^{on}t_f e^{-\frac{t_f}{\tau_2^{on}}} \\
 &- A_1^{on}\tau_1^{on}\left(e^{-\frac{t_f}{\tau_1^{on}}} - 1\right) \\
 &- A_2^{on}\tau_2^{on}\left(e^{-\frac{t_f}{\tau_2^{on}}} - 1\right) \tag{10}
 \end{aligned}$$

and in the limit  $t_f \rightarrow \infty$  then the oxygen deficit approaches  $O_{2_{trad}}^{defi} = A_1^{on}\tau_1^{on} + A_2^{on}\tau_2^{on}$ .

We now calculate the oxygen debt,  $O_2^{debt}$ , in the same way as above using Eq. (2). We have  $EE\dot{V}O_2 - A_{0_n}^{off} - A_{1_n}^{off} - A_{2_n}^{off} = \dot{V}O_{2b}$  where  $\dot{V}O_{2b}$  is the baseline or minimum resting value of oxygen uptake.

$$\begin{aligned}
 O_2^{debt} &= (A_{0_n}^{off} + A_{1_n}^{off} + A_{2_n}^{off})TD^{off} \\
 &+ (A_{1_n}^{off} + A_{2_n}^{off})(t_f - TD^{off})
 \end{aligned}$$

$$\begin{aligned}
 & - \int_{t_0=0}^{TD^{off}} A_0^{off} \left( 1 - e^{-\frac{t}{\tau_0^{off}}} \right) dt \\
 & - \int_{TD^{off}}^{t_f} A_1^{off} \left( 1 - e^{-\frac{(t-TD^{off})}{\tau_1^{off}}} \right) dt \\
 & - \int_{TD^{off}}^{t_f} A_2^{off} \left( 1 - e^{-\frac{(t-TD^{off})}{\tau_2^{off}}} \right) dt
 \end{aligned} \tag{11}$$

which upon solving the integrals gives

$$\begin{aligned}
 O_2^{debt} &= A_0^{off} \tau_0^{off} \left( 1 - e^{-\frac{TD^{off}}{\tau_0^{off}}} \right) \\
 & - A_0^{off} TD^{off} e^{-\frac{TD^{off}}{\tau_0^{off}}} \\
 & + A_1^{off} \tau_1^{off} \left( 1 - e^{-\frac{(t_f-TD^{off})}{\tau_1^{off}}} \right) \\
 & + A_1^{off} (TD^{off} - t_f) e^{-\frac{(t_f-TD^{off})}{\tau_1^{off}}} \\
 & + A_2^{off} \tau_2^{off} \left( 1 - e^{-\frac{(t_f-TD^{off})}{\tau_2^{off}}} \right) \\
 & + A_2^{off} (TD^{off} - t_f) e^{-\frac{(t_f-TD^{off})}{\tau_2^{off}}} .
 \end{aligned} \tag{12}$$

If we remove the first phase (as in [Bearden and Moffatt \(2000\)](#) where phase 3 is also removed) and set  $t_0 = TD^{off} = 0$ , then in the limit  $t_f \rightarrow \infty$  the oxygen debt approaches  $O_2^{debt} = A_1^{off} \tau_1^{off} + A_2^{off} \tau_2^{off}$ . The oxygen debt will therefore be equal to the deficit if  $A_1^{on} \tau_1^{on} + A_2^{on} \tau_2^{on} = A_1^{off} \tau_1^{off} + A_2^{off} \tau_2^{off}$  under the assumptions that  $A_0^{on} = A_0^{off} = 0$  and we have a common time delay such that  $TD_1^{on} = TD_2^{on} = TD^{on}$ ,  $TD_1^{off} = TD_2^{off} = TD^{off}$  where  $t_0^{on} = TD^{on} = 0$  and  $t_0^{off} = TD^{off} = 0$ . The oxygen consumed in recovery,  $O_2^{rec}$ , can be obtained ([Bearden and Moffatt, 2000](#)) by adding  $(EE\dot{V}O_2 - A_{0_n}^{off} - A_{1_n}^{off} - A_{2_n}^{off})(t_f - t_0)$  to Eqs. (11) and (12).

It can be seen that there are many major problems with the models just presented, not least the use of phases to model the time series of  $\dot{V}O_2(t)$ . One of the other major problems is that  $A_i^{on/off}$ ,  $TD_i^{on/off}$ ,  $\tau_i^{on/off}$ , for  $i = 0, 1, 2$ , should in fact be variables which depend on the exercise intensity. This can easily be realized as these so-called parameters can be seen to change with change in the intensity of the exercise. Due to this, the model previously described cannot be used to predict the  $\dot{V}O_2(t)$ , given the time series for the intensity  $v(t)$ . It can only fit curves through existing data with the parameters being compared to give physiological significance. We go on to address these issues in the next section where we present a new model in the form of a dynamical system, where the  $\dot{V}O_2(t)$  is coupled to the exercise intensity.

### 3. A new model for the $\dot{V}O_2(t)$ kinetics

We first develop a model for the underlying dynamics or basic response pattern of the oxygen uptake kinetics using a set of coupled ordinary differential equations similar to those used by the authors to model different nonlinear time series (Stirling and Zakythinaki, 2004, submitted for publication; Stirling, 2000, 2003). We then go on to give solutions for calculating the time series of the oxygen demand and hence as a result the deficit and debt.

#### 3.1. The equations

$\dot{V}O_2(v, t)$  represents the time series for the oxygen uptake kinetics which changes with both time  $t$  and exercise intensity,  $v$ . We make use of and focus on the fact that the rate of increase of the oxygen uptake kinetics,  $\ddot{V}O_2(v, t)$ , goes to zero for three specific oxygen demands. These demands are the minimum resting value of oxygen uptake,  $\dot{V}O_{2\min}$ , the maximum value,  $\dot{V}O_{2\max}$ , and a sub-maximal oxygen demand,  $D(v, t)$ , the magnitude of which depends on the exercise intensity and maybe duration. Note that if  $D(v, t) \geq \dot{V}O_{2\max}$ , then  $\dot{V}O_2(v, t)$  approaches zero as we approach  $\dot{V}O_{2\max}$ . The other main consideration is that there is  $\dot{V}O_{2\min} \leq \dot{V}O_2(v, t) \leq \dot{V}O_{2\max}$ . Note that the fact that the  $\dot{V}O_2(v, t) \geq \dot{V}O_{2\min}$  is the other reason that  $\ddot{V}O_2(v, t) = 0$  when  $\dot{V}O_2(v, t) = \dot{V}O_{2\min}$ ; otherwise we could get values of  $\dot{V}O_2(v, t) < \dot{V}O_{2\min}$  which would not be physiologically realistic. We model the uptake kinetics in the following manner, where we assume that the rate of increase in  $\dot{V}O_2(v, t)$  is a function of the current value of the  $\dot{V}O_2(v, t)$ , the intensity of the exercise (i.e. the speed,  $v$ ) and time. This is supported by the observation (Astrand and Saltin, 1961; Linnarsson, 1974; Saltin, 1990) that the rate of rise of oxygen uptake at the onset of exercise is a function of relative exercise intensity and also that  $\dot{V}O_{2\max}$  is more rapidly attained as the supra-maximal workload becomes higher (Astrand and Saltin, 1961; Margaria et al., 1965). Also Hill and Stevens (2001) conclude that “at the onset of exercise in the severe intensity domain,  $\dot{V}O_2$  is initially driven toward the  $O_2$  demand, and then is limited by the achievable  $\dot{V}O_2$ , the  $\dot{V}O_{2\text{peak}}$ ”, where  $\dot{V}O_{2\text{peak}} = \dot{V}O_{2\max}$  unless we have premature fatigue. Also phenomena such as the  $\dot{V}O_2$  drift, where the oxygen uptake increases over time for long duration steady exercise intensities below the so-called lactate threshold, can be thought of as resulting from an increase in the oxygen demand  $D(v, t)$  with time,  $t$ , for  $v$  constant.

The model is given by

$$\ddot{V}O_2(v, t) = A(\dot{V}O_2(v, t) - \dot{V}O_{2\min})^B (\dot{V}O_{2\max} - \dot{V}O_2(v, t))^C \times (D(v, t) - \dot{V}O_2(v, t))^E \quad (13)$$

$$\dot{v} = I(t). \quad (14)$$

The vector  $\dot{v} = I(t)$  defines the rate of change of intensity or speed. For linear exercise intensities we have  $\dot{v} = c$  where  $c$  is a constant, with  $c = 0$  for the constant speed or steady-state case. For simplicity and numerical reasons we assume dimensionless quantities and normalize the  $\dot{V}O_2(v, t)$  such that  $0 \leq \dot{V}O_2(v, t) \leq 1$ , i.e.  $\dot{V}O_{2\min} = 0$  and  $\dot{V}O_{2\max} = 1$ .

Eqs. (13) and (14) take the form

$$\dot{V}O_2(v, t) = A(\dot{V}O_2(v, t))^B(1 - \dot{V}O_2(v, t))^C(D(v, t) - \dot{V}O_2(v, t))^E \tag{15}$$

$$\dot{v} = I(t). \tag{16}$$

The function  $D(v, t) \geq 0$  is the function describing the oxygen demand of the exercise. Note that we will have  $D(v, t) \geq 1$  for values of severe or very high intensity exercise and this will result in a peak  $\dot{V}O_2(v, t)$  equal to  $\dot{V}O_{2max}$  assuming that the exercise can be continued for a sufficiently long time period. We have  $D(v, t) = 1$  when  $v = v_{min} \dot{V}O_{2max}$  (i.e. the minimum value of the speed or intensity for which we can achieve  $\dot{V}O_{2max}$  inclusive of the slow component). This can be used to fit the parameters of the model. In particular we can use the time that it takes to achieve  $\dot{V}O_{2max}$  with the minimum intensity possible. The value of the speed is found to be slightly (i.e. somewhere before the next speed increment) above that of the so-called critical speed; see Section 1.1. Above the critical speed (i.e. during high intensity exercise) the  $\dot{V}O_2(v, t)$  is not stabilized and hence the  $\dot{V}O_2(v, t)$  continues to rise until it reaches the  $\dot{V}O_{2max}$  unless fatigue sets in before  $\dot{V}O_{2max}$  can be achieved.

$A, B, C, E$  are parameters which can be used to change the shape of the curve. In Eqs. (13) and (14) the parameters  $B, C$  and  $E$  are dimensionless whilst parameter  $A$  has dimensions of  $(m^3s^{-1})^{(1-B-C-E)}s^{-1}$ . Parameter  $A$  (where  $A > 0$  always) modifies how steeply the curve rises (i.e., the magnitude of the rate of change of  $\dot{V}O_2(v, t)$ ) and as a result the time taken to reach the steady-state value  $\dot{V}O_{2ss}$ .  $B$  controls how quickly we leave or approach the minimum value  $\dot{V}O_{2min}$ .  $C$  controls how quickly we approach or leave the maximum value  $\dot{V}O_{2max}$ .  $E$  cannot be even or a fraction. Notice that if we put  $B = C = 0$  we get the plateau-type curves that are classically expected below the lactate threshold.  $B \neq 0$  and  $C \neq 0$  however give a curve which takes much longer to plateau off for values of  $\dot{V}O_2(v, t)$  close to  $\dot{V}O_{2max}$ . This is very similar to the effect that the so-called slow component has on the  $\dot{V}O_2(v, t)$  kinetics.

The values of the positive parameters  $A, B, C, E$  can be determined for exercises where the oxygen demand is such that  $D(v, t) \ll \dot{V}O_{2max}$ . For such intensities it is believed that the value of the demand,  $D(v, t)$ , is to a good approximation constant and equal to the end of the exercise steady state,  $\dot{V}O_{2ss}$ , which can be obtained from the time series of the  $\dot{V}O_2(v, t)$ . Note that this is probably true for exercise intensities such that  $D(v, t) \ll \dot{V}O_{2max}$ . For higher values of  $D(v, t)$ , especially for the cases were  $D(v, t) > \dot{V}O_{2max}$ , the oxygen demand is probably a function of time. As the intensity of the exercise becomes closer to our absolute speed limit we will become less efficient the longer we exercise at that intensity. This could result in a time dependent behavior in the oxygen demand  $D(v, t)$ .

We now go on to explain how to calculate the linear stability of the fixed point solutions of our system.

### 3.2. Solution for fixed points and how to set the values of the parameters

In a model of coupled ordinary differential equations such as (13) and (14) fixed points occur when  $\dot{V}O_2 = \dot{v} = 0$ . If  $v = c$  where  $c$  is a constant, then for that particular intensity the oxygen demand and uptake are functions of time such that  $D(v, t) = D(t)$

and  $\dot{V}O_2(v, t) = \dot{V}O_2(t)$  respectively. For these conditions there are three solutions to  $\ddot{V}O_2 = 0$ , the first being  $\dot{V}O_2(t) = \dot{V}O_{2\min}$ , the second being  $\dot{V}O_2(t) = \dot{V}O_{2\max}$  and the third being  $\dot{V}O_2(t) = D(t)$ . We solve for the linear stability of these fixed points to find how orbits nearby behave. This can be used to fit the values of the parameters  $A, B, C, E$ .

The Jacobian matrix,  $J$ , is

$$J = \begin{pmatrix} \frac{\partial \ddot{V}O_2(t)}{\partial \dot{V}O_2(t)} & \frac{\partial \ddot{V}O_2(t)}{\partial v} \\ \frac{\partial \dot{v}}{\partial \dot{V}O_2(t)} & \frac{\partial \dot{v}}{\partial v} \end{pmatrix} \tag{17}$$

and the eigenvalues  $\lambda$  of the Jacobian matrix  $J$  are

$$\lambda = \frac{\frac{\partial \ddot{V}O_2(t)}{\partial \dot{V}O_2(t)} + \frac{\partial \dot{v}}{\partial v} \pm \sqrt{\left(\frac{\partial \ddot{V}O_2(t)}{\partial \dot{V}O_2(t)} - \frac{\partial \dot{v}}{\partial v}\right)^2 + 4 \frac{\partial \ddot{V}O_2(t)}{\partial v} \frac{\partial \dot{v}}{\partial \dot{V}O_2(t)}}}{2} \tag{18}$$

As, however,  $\dot{v}$  is a function of neither  $\dot{V}O_2(t)$  nor  $v$ , we have  $\frac{\partial \dot{v}}{\partial \dot{V}O_2(t)} = 0$  and  $\frac{\partial \dot{v}}{\partial v} = 0$ ; hence

$$\lambda_1 = 0$$

and

$$\begin{aligned} \lambda_2 &= \frac{\partial \ddot{V}O_2(t)}{\partial \dot{V}O_2(t)} \\ &= Af^{B-1}g^{C-1}h^{E-1}[Bgh - Cfh - Efg] \end{aligned} \tag{19}$$

where

$$\begin{aligned} f &= \dot{V}O_2(t) - \dot{V}O_{2\min}, \\ g &= \dot{V}O_{2\max} - \dot{V}O_2(t), \\ h &= D(t) - \dot{V}O_2(t). \end{aligned} \tag{20}$$

For  $B \neq 1, C \neq 1, E \neq 1$ , we have  $\lambda_2 = \frac{\partial \ddot{V}O_2(t)}{\partial \dot{V}O_2(t)} = 0$  for our fixed point solutions, as  $f = 0, g = 0$  and  $h = 0$  when  $\dot{V}O_2(t) = \dot{V}O_{2\min}, \dot{V}O_2(t) = \dot{V}O_{2\max}$  and  $\dot{V}O_2(t) = D(t)$  respectively. This means that the solutions for the three fixed points in our system would all have  $\lambda_{1,2} = 0$ ; hence they are neutral fixed points. If we decide that we need non-neutral solutions, however, we need at least one of  $B, C$  and  $E$  to be equal to 1, depending on which solutions we need to be attracting. Depending on the data that we model however it may be more important to be able to manipulate the vector fields by changing the values of  $B, C$  and  $E$  than to be concerned with the fact that the three solutions are neutral with  $\lambda_1 = \lambda_2 = 0$ . What we choose for the values of the parameters therefore will depend on the data that we are modelling.

*3.2.1. Solutions for  $\lambda_2$  when  $B \neq 1, C = 1, E = 1$*

If we have  $B \neq 1, C = 1, E = 1$ , then this allows us to have attracting solutions and also gives us freedom regarding the rate of attraction to the sub-maximal steady-state

solutions as we shall see later on. Notice that putting  $C \neq 1$  and or  $E \neq 1$  does not give us this freedom; it would however give us more freedom in changing the shape of the curve for the  $\dot{V}O_2(t)$  time series when we are far from the three solutions previously mentioned. We now have

$$\lambda_2 = \frac{\partial \dot{V}O_2(t)}{\partial \dot{V}O_2(t)} = Af^{B-1}[Bgh - fh - fg]. \tag{21}$$

This has four solutions of interest:

When  $\dot{V}O_2(t) = \dot{V}O_{2max}$ , and hence  $g = 0$ , we have

$$\begin{aligned} \lambda_2 &= -Af^B h \\ &= -A(\dot{V}O_{2max} - \dot{V}O_{2min})^B (D(t) - \dot{V}O_{2max}) \end{aligned} \tag{22}$$

which becomes  $\lambda_2 = -A(D(t) - 1)$  in our normalized equations.

For  $D(t) = \dot{V}O_{2max}$ , the solution is neutral, i.e.  $\lambda_2 = 0$ .

If however  $D(t) > \dot{V}O_{2max}$ , then the solution  $\dot{V}O_2(t) = \dot{V}O_{2max}$  is an attractor, the strength of which increases the more  $D(t)$  is greater than  $\dot{V}O_{2max}$ . For  $\dot{V}O_2(t) = \dot{V}O_{2min}$ ,  $f = 0$  and practically we must also have  $D(t) = \dot{V}O_{2min}$  and hence  $h = 0$ . Therefore  $\lambda_2 = 0$  and the solution is neutral.

For  $\dot{V}O_2(t) = D(t)$  and  $\dot{V}O_{2min} < D(t) < \dot{V}O_{2max}$  we have  $h = 0$ . We therefore have

$$\begin{aligned} \lambda_2 &= -Af^B g \\ &= -A(D(t) - \dot{V}O_{2min})^B (\dot{V}O_{2max} - D(t)) \end{aligned} \tag{23}$$

and hence, as  $\lambda_2 < 0$  for  $\dot{V}O_{2min} < D(t) < \dot{V}O_{2max}$  and  $A > 0$ , this solution is attracting, with  $\lambda_2$  approaching zero as  $D(t)$  approaches  $\dot{V}O_{2min}$  or  $\dot{V}O_{2max}$ . We have  $\lambda_2 = -A(D(t))^B (1 - D(t))$ , with  $0 < D(t) < 1$  for the normalized solutions.

This means that  $\lambda_1 = 0$  always but  $\lambda_2 = 0$  only when  $\dot{V}O_2(t) = \dot{V}O_{2min} = D(t)$  or  $\dot{V}O_2(t) = \dot{V}O_{2max} = D(t)$ . For  $\dot{V}O_2(t) = D(t)$  and  $\dot{V}O_{2min} < D(t) < \dot{V}O_{2max}$  or  $D(t) > \dot{V}O_{2max}$ , the solution is an attractor, the strength of which depends on the magnitude of both  $A$  and  $B$  and also the magnitude of  $D(t)$  or  $D(t)$  relative to the  $\dot{V}O_{2min}$  and  $\dot{V}O_{2max}$ .

Assuming that we have  $C = E = 1$  and  $\dot{V}O_2(t) = D(t)$  we can use Eq. (23) to fit the value of the parameter  $B$  in the following way:

$$\begin{aligned} \frac{\partial \lambda_2}{\partial D(t)} &= A(D(t) - \dot{V}O_{2min})^{B-1} \\ &\times [D(t)(B + 1) - \dot{V}O_{2min} - B\dot{V}O_{2max}]. \end{aligned} \tag{24}$$

To find the particular value of  $D(t)$  where  $\lambda_2$  is a minimum (which we define as  $D(t) = D_c^{\lambda_2turn}$ ) in the range  $\dot{V}O_{2min} \leq D(t) \leq \dot{V}O_{2max}$ , we solve for the turning point where  $\frac{\partial \lambda_2}{\partial D(t)} = 0$ :

$$A(D_c^{\lambda_2turn} - \dot{V}O_{2min})^{B-1} [D_c^{\lambda_2turn} (B + 1) - \dot{V}O_{2min} - B\dot{V}O_{2max}] = 0 \tag{25}$$

which has two trivial solutions,  $A = 0$ ,  $D_c^{\lambda_2 \text{turn}} = \dot{V}O_{2\text{min}}$ , and one nontrivial solution,

$$D_c^{\lambda_2 \text{turn}} = \frac{\dot{V}O_{2\text{min}} + B\dot{V}O_{2\text{max}}}{B + 1}. \tag{26}$$

Using solution (26) we can change the value of  $B$  so as to change the value of  $D_c^{\lambda_2 \text{turn}}$  for which the attraction is a maximum, and hence  $\lambda_2$  is a minimum, in the range  $\dot{V}O_{2\text{min}} \leq D_c^{\lambda_2 \text{turn}} \leq \dot{V}O_{2\text{max}}$ . Solution (26) becomes  $D_c^{\lambda_2 \text{turn}} = \frac{B}{B+1}$  with  $0 \leq D_c^{\lambda_2 \text{turn}} \leq 1$  in the normalized case.

*3.2.2. Solutions for  $\lambda_2$  when  $B \neq 1$ ,  $C \neq 1$ ,  $E = 1$*

If we have the parameters  $B \neq 1$ ,  $C \neq 1$  and  $E = 1$ , then using Eq. (20) we have  $\lambda_2 = 0$  for  $\dot{V}O_2(t) = \dot{V}O_{2\text{min}}$  and  $\dot{V}O_2(t) = \dot{V}O_{2\text{max}}$ , whilst for  $\dot{V}O_2(t) = D(t)$  we have

$$\lambda_2 = -A f^B g^C \\ = -A(D(t) - \dot{V}O_{2\text{min}})^B (\dot{V}O_{2\text{max}} - D(t))^C. \tag{27}$$

This gives us an attracting solution for  $A > 0$  as  $\dot{V}O_{2\text{min}} < D(t) < \dot{V}O_{2\text{max}}$ . The values of  $D(t) = D_c^{\lambda_2 \text{turn}}$  for which  $\lambda_2$  is a minimum are found as before from the turning point, i.e. where

$$\frac{\partial \lambda_2}{\partial D(t)} = A(D(t) - \dot{V}O_{2\text{min}})^{B-1} (\dot{V}O_{2\text{max}} - D(t))^{C-1} \\ \times [C(D(t) - \dot{V}O_{2\text{min}}) - B(\dot{V}O_{2\text{max}} - D(t))] = 0 \tag{28}$$

which has trivial solutions at  $D(t) = \dot{V}O_{2\text{min}}$  and  $D(t) = \dot{V}O_{2\text{max}}$  and a nontrivial solution at  $D(t) = D_c^{\lambda_2 \text{turn}} = \frac{B\dot{V}O_{2\text{max}} + C\dot{V}O_{2\text{min}}}{B+C}$ , which gives  $D_c^{\lambda_2 \text{turn}} = \frac{B}{B+C}$  in the normalized case. This relationship can then be used to fit the values of  $B$  and  $C$ .

*3.2.3. How to choose  $A$*

The parameter  $A$  is chosen so as to enable us to reach the  $\dot{V}O_{2\text{ss}}$  after the correct period of time,  $t$ . By increasing the value of  $A$  we decrease the amount of time needed to reach a particular steady state  $\dot{V}O_{2\text{ss}}$ .

*3.2.4. An example*

We show example time series for the  $\dot{V}O_2(t)$  at different constant exercise intensities,  $v = c$ . See Fig. 3 for the on-transient kinetics and Fig. 4 for the off-transient kinetics. We make the traditional assumption, for the purpose of this example, that the oxygen demand for each intensity is a constant function of time, and hence the demand becomes  $D_c$  as  $\dot{v} = 0$ . We set the parameters  $B > 1$  and  $C = E = 1$ , for the normalized Eqs. (15) and (16). Using suitable values for the parameters such that  $A = 10$  and  $B = 2$  we then numerically integrate  $\dot{V}O_2(t)$  with respect to time to obtain the  $\dot{V}O_2(t)$  time series for different oxygen demands,  $D_c$ , and initial conditions,  $\dot{V}O_2(0)$ .

For an example of the case where  $C \neq 1$ ,  $B \neq 1$  and  $E = 1$ , see Figs. 5 and 6, in which we choose  $A = 10$ ,  $B = 0.9$ ,  $C = 1.25$  and  $E = 1$ . As can be seen by comparing Figs. 3 and 5 for the on-transient kinetics and Figs. 4 and 6 for the off-transient kinetics, allowing  $C \neq 1$  and  $B \neq 1$  gives us more freedom to change the vector field and hence the shape

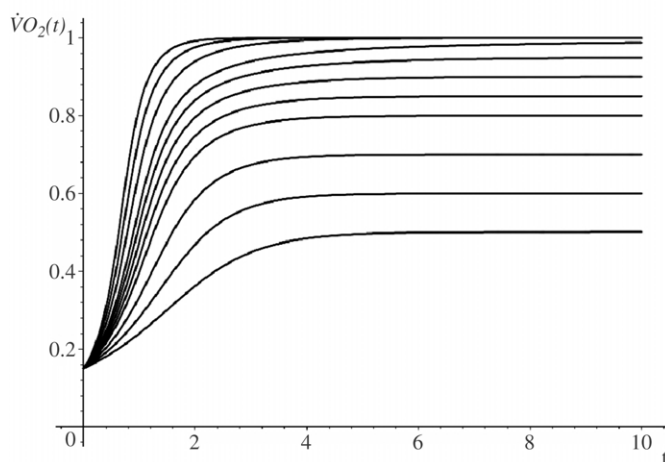


Fig. 3. The on-transient oxygen uptake kinetics obtained using the normalized Eqs. (15) and (16), with  $A = 10$ ,  $B = 2$  and  $C = E = 1$ . Each curve represents the  $\dot{V}O_2(t)$  for different steady-state oxygen demands given the same initial condition.

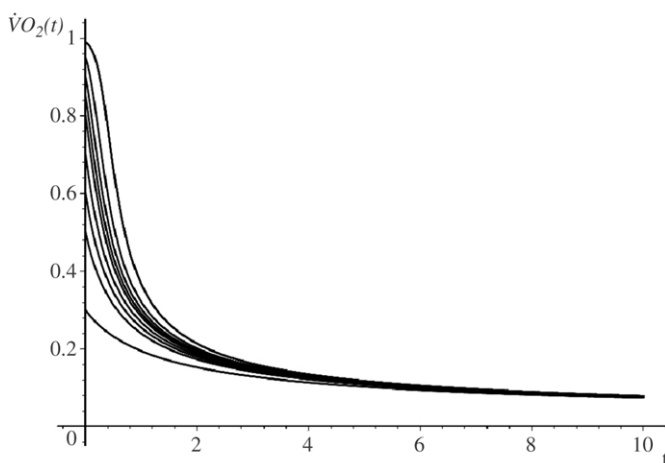


Fig. 4. The off-transient oxygen uptake kinetics obtained using the normalized Eqs. (15) and (16), with  $A = 10$ ,  $B = 2$  and  $C = E = 1$ . Each curve represents the  $\dot{V}O_2(t)$  for different initial conditions (end of hard exercise, beginning of recovery) and identical steady-state oxygen demands, where the oxygen demand is equal to the baseline  $\dot{V}O_{2b}$ , i.e.  $D(t) = 0$ .

of the  $\dot{V}O_2(t)$  curve. In particular one can see that we can accelerate the way orbits leave very low initial conditions and give a more pronounced slowing down of the kinetics as we approach maximum values.

In all the Figs. 3–6 it can be seen that we can generate the type of behavior known as the slow component. This can be seen in the figures as a slowing down of the uptake kinetics

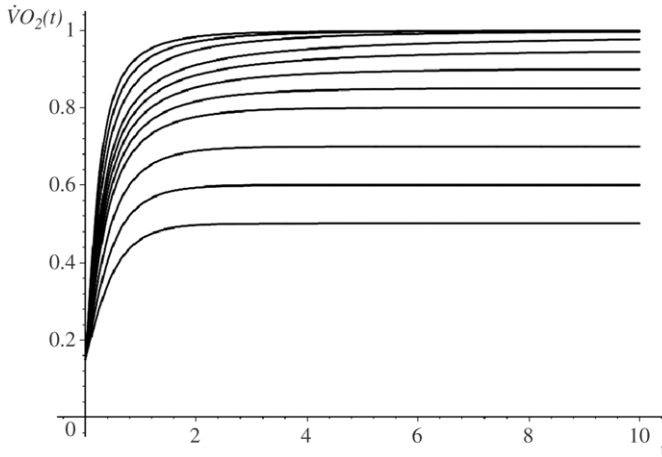


Fig. 5. The on-transient oxygen uptake kinetics obtained using the normalized Eqs. (15) and (16), with  $A = 10$ ,  $B = 0.9$ ,  $C = 1.25$  and  $E = 1$ . Each curve represents the  $\dot{V}O_2(t)$  for different steady-state oxygen demands given the same initial condition.

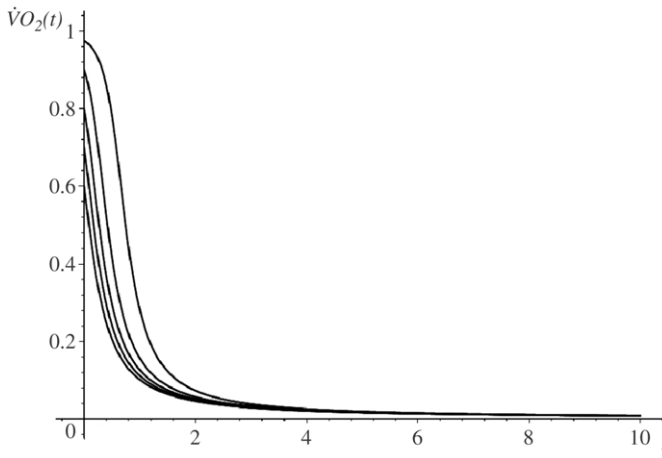


Fig. 6. The off-transient oxygen uptake kinetics obtained using the normalized Eqs. (15) and (16), with  $A = 10$ ,  $B = 0.9$ ,  $C = 1.25$  and  $E = 1$ . Each curve represents the  $\dot{V}O_2(t)$  for different initial conditions (end of hard exercise, beginning of recovery) and identical steady-state oxygen demands, where the oxygen demand is equal to the baseline  $\dot{V}O_{2b}$ , i.e.  $D(t) = 0$ .

as we approach either the  $\dot{V}O_{2\max}$  in the case of the on-transient, or the  $\dot{V}O_{2\min}$  in the case of the off-transient. What can also be seen in the figures is that the underlying dynamics of the  $\dot{V}O_2(t)$  kinetics can be modelled by a curve which is a smooth function of time,  $\dot{V}O_2$  and intensity and does not contain any phases or time delays.

**4. Finding the oxygen demand  $D(v, t)$  and the resulting solutions for oxygen deficit and debt**

If we look at Eqs. (13) and (14) we see that given the time series of the  $\dot{V}O_2(t)$  kinetics for a range of different velocities or intensities, we can calculate the oxygen demand, and hence the debt and deficit once we have found the values of the parameters  $A, B, C, E$ . These can be found for the cases where we know the value of the demand  $D_c$ , i.e. those low constant intensity cases (i.e.  $v = c$ ) where we have a sub-maximal steady state for the  $\dot{V}O_2(t)$  and hence we can assume that the oxygen demand is not a function of time (see Section 1.3); therefore we have  $D(v, t) = D_c = \dot{V}O_{2_{ss}}$ . It should be noted that we can always collect data from enough steady-state cases to be able to fit the parameters. The other quantity that we use to fit the parameter is the time  $t$  that it takes to achieve certain values of the  $\dot{V}O_2$ . In particular this can be used to determine the value of parameter  $A$ .

Let us assume that the time series of the data correspond to a set of  $N$  values recorded at each time  $t^k, k = 0, \dots, N - 1$ , where  $t_0 = 0$  (beginning of exercise) and  $t_{N-1} = t_f$  (end of exercise). The data for  $\dot{V}O_2$  are in the form of the time series

$$\dot{V}O_2^k \equiv \dot{V}O_2(t^k), \quad k = 0, \dots, N - 1.$$

We consider that the  $\dot{V}O_2$  data oscillates with a high amplitude and frequency around a smooth curve which is a function of both time and intensity. To remove these high frequency oscillations and find the smooth underlying curve, we follow a method based on the frequency components of a signal, which can be used to delete the higher harmonics and to reconstruct the signal from the lowest harmonics. A detailed description of this curve-smoothing (filtering) method can be found in [Zakynthinaki and Stirling \(submitted for publication\)](#) and [Stirling and Zakynthinaki \(submitted for publication\)](#), where the authors apply similar techniques to smooth the heart rate time series in response to exercise, which is very similar to the type of time series that we deal with here.

Let us denote as  $[\dot{V}O_2^k]_f$  the smoothed (filtered) time series of the  $\dot{V}O_2$  data. The derivative of the  $[\dot{V}O_2^k]_f$  data can be easily computed numerically (see the [Appendix](#)) resulting in a time series  $\ddot{V}O_2^k \equiv \ddot{V}O_2(t^k) (k = 0, \dots, N - 1)$  of  $\dot{V}O_2$ .

*4.1. Derivation of the function  $D(v, t)$*

Let us assume that we have a set of  $M$  exercises, each of which is performed with a steady-state exercise intensity (i.e. constant speed)  $v = v_i = \text{constant}$ , where  $i = 1, \dots, M$ . We assume that for each exercise the time series  $\dot{V}O_2^k \equiv \dot{V}O_2(v_i, t^k), k = 0, \dots, N - 1$ , are known (calculated as in the [Appendix](#)). Let us denote as  $D_i(t)$  the function describing the demand of the  $i$ th exercise ( $i = 1, \dots, M$ ). We can then denote the time series of the demand of this particular exercise as  $D_i^k$ , where  $D_i^k \equiv D(v_i, t^k)$ .

For each time step and each steady-state intensity, Eq. (13) becomes

$$\begin{aligned} \ddot{V}O_2^k &= A([\dot{V}O_2^k]_f - \dot{V}O_{2_{\min}})^B \\ &\times (\dot{V}O_{2_{\max}} - [\dot{V}O_2^k]_f)^C (D_i^k - [\dot{V}O_2^k]_f)^E \\ & \quad i = 1, \dots, M \quad k = 0, \dots, N - 1 \end{aligned} \tag{29}$$

where the parameters  $A, B, C$  and  $E$  have been calculated for the case such that  $D(v, t) \ll \dot{V}O_{2\max}$  and hence  $\dot{V}O_{2ss} = D(v)$ . From Eq. (29) the values  $D_i^k$  can be calculated for each time step  $k$ .

From the set of  $N$  points  $\{(t^k, D_i^k), k = 0, \dots, N - 1\}$  the function  $D(v_i, t)$  can be numerically approximated, for each constant speed  $v_i$ , using a modelling procedure such as the least-squares one for a linear approximation, or if necessary a more advanced numerical fitting method (see Press et al. (1993)). Similarly, for each time step  $t^k$ , the function  $D(v, t^k)$  can be numerically approximated from the set of  $M$  points  $\{(v_i, D_i^k), i = 1, \dots, M\}$ . The above procedure will finally give the function  $D(v, t)$ .

Regarding now the case where, after a time step  $m$  (where  $0 \leq m \leq N - 1$  and so  $t_m < t_f$ ), there is  $\dot{V}O_2(t) = \dot{V}O_{2\max}$ , and hence  $\ddot{V}O_2 = 0$ , we work as follows. The function  $D(v, t)$  can be numerically approximated from the set of points  $\{v_i, D_i^k\}$  as follows:

- For  $0 \leq k < m$  (where still  $\ddot{V}O_2 \neq 0$ ) the points  $D(v, t^k)$  can be numerically approximated from the set of points  $\{v_i, D_i^k\}$ , by applying a numerical fitting method, as described before.
- For  $m \leq k \leq N - 1$ , the points  $D(v, t^k)$  can be approximated by extrapolating the already existing set of points  $\{v_i, D_i^k\}, 0 \leq k < m$ . For the extrapolation various numerical techniques can be applied, such as a Neville iterated polynomial extrapolation or a Hermite polynomial extrapolation (Press et al., 1993).

#### 4.2. Calculating the oxygen deficit $O_2^{defi}$ and debt $O_2^{debt}$

We now have a method for calculating the oxygen demand from the rate of increase in  $\dot{V}O_2(t)$  (i.e. the  $\ddot{V}O_2(t)$ ) for the full range of exercise intensities, including severe exercise where the demand is above the  $\dot{V}O_{2\max}$ . With the knowledge of this we can calculate numerically via an integration the deficit/debt at all exercise intensities.

Let us denote by  $v^{on}$  the exercise intensity for the on-transient and  $v^{off}$  that for the off-transient or the recovery intensity. If  $D^{k^{on}} \equiv D(v^{on}, t^k)$  and  $D^{k^{off}} \equiv D(v^{off}, t^k)$  the oxygen deficit is given by

$$O_2^{defi} = \sum_{k=0}^{N-1} (D^{k^{on}} - [\dot{V}O_2^k]_f) \tag{30}$$

while the oxygen debt,  $O_2^{debt}$ , is given by

$$O_2^{debt} = \sum_{k=0}^{N-1} ([\dot{V}O_2^k]_f - D^{k^{off}}) \tag{31}$$

where  $D^{k^{off}}$  is constant and equal to the basal recovery oxygen consumption (i.e.  $v^{off} = 0$ ). The oxygen consumed in recovery is given by

$$O_2^{rec} = \sum_{k=0}^{N-1} [\dot{V}O_2^k]_f. \tag{32}$$

## 5. Conclusions

In this paper we show three main things.

- We present a new model in the form of a dynamical system for the underlying dynamics of the oxygen uptake kinetics in response to exercise. This is the first time that a model of this kind which does not use phases or, more importantly, time delays has been used.
- We show how to obtain the time series for the oxygen demand from the time series of the oxygen uptake,  $\dot{V}O_2(v, t)$ .
- We show how this can be used to calculate the oxygen deficit and debt. We compare our model with the existing three-phase model and give for the first time complete analytic solutions for the oxygen deficit and debt. We also explain the physiological processes involved.

The model that we present is of vast use for exercise intensities where the oxygen demand is above the  $\dot{V}O_{2\max}$  as we do not need to use the linear extrapolation usually used. It is believed that this linear extrapolation of the demand from sub-maximal values underestimates the demand as it does not account for losses in efficiency etc. at very high almost maximal work loads. As a result, by using our methods to calculate the oxygen demand  $D(v, t)$ , we can also give far more accurate estimations of the oxygen debt and deficit. This can be very useful for improving our understanding of the anaerobic contribution to exercise.

Once we have fitted the parameters and found the function  $D(v, t)$ , one of the major advantages of our model is that, given a new speed time series, we can make predictions as regards the resulting  $\dot{V}O_2(v, t)$  time series and hence predict the oxygen deficit and debt. This was not possible before with the three-phase model, as that model only allowed one to fit curves to given data. We can also calculate  $\dot{V}O_2(v, t)$  when the derivative of the intensity is a function of time, i.e.  $\dot{v} = I(t)$ . This would allow us to investigate the response to exercise intensities which are both linear and nonlinear functions of time. This of course would be very important, as in reality the intensity of the exercise in most training and competition situations is not in the form of a square wave or constant. This is also important from the point of view of nonlinear dynamics, as the response of two coupled nonlinear systems can be far more complicated than what could be predicted from the usually studied response to a linear exercise intensity.

Regarding the three-phase model and the model and methods that we propose, we make the following comments.

- The procedure of enhancing the basic response pattern via averaging repeated identical experiments has many serious problems associated with it. To name and treat the oscillations as noise is incorrect as they contain basic features of the signal, as is the case in many nonlinear systems, and not just a property of errors in the measuring devices. By averaging repeated identical experiments it is possible to remove these fluctuations and other noise in the system but it is also possible to produce an averaged system which has features not found in the original non-averaged signals. It is therefore not correct or useful to state that there exist three phases underlying the response to a bout of exercise if these can only be observed in the averaged system. It is also misleading to use a system which has been averaged in this manner to support the

existence of different phases of physiological behavior, especially when these phases are treated as separate entities which start after discrete time intervals and add together in a non-smooth building block manner. We argue that a more rigorous and useful way to filter the data and hence obtain the underlying signal is to remove the high frequency oscillations using Fourier analysis (Zakynthinaki and Stirling, submitted for publication). This will give us the low frequency harmonics in the signal and hence the curve about which the noise is distributed during an individual bout of exercise.

- The use of three phases which turn on and off after different time delays also has problems associated with it. Such a system is of most use when the phases are very well defined such as in the solid to liquid and liquid to gas phases in water. In the responses that we model however, the so-called phases are not so well defined and the response appears to be far more suited to being modelled by a continuous differential function over the whole range of the three phases. It is also unclear whether these three distinct phases provide a good model of the physiological processes, for the reason mentioned above and also because once phase 2 has finished, for example, it plays no further part in the dynamics. This is a very strong condition to impose on the model and also it is not the sort of behavior that one usually associates with the kinds of dynamical systems that we consider here. Instead it would be better to model the system as a smooth and continuous function of such variables as  $\dot{V}O_2$ , intensity and time.
- After editing and then averaging the data over repeated exercise bouts, it was shown by (Barstow and Mole, 1991) that the family of exponentials that they were using in their model fitted better if the time delay for the third phase was longer than that for the second phase. This does not mean however that one could not model the curve as a smooth function of time and intensity with other families of curves such as the one that we present here or such as the curve resulting from the sum of the low frequency exponentials of a Fourier reconstruction and filtering of the raw data (Zakynthinaki and Stirling, submitted for publication). In fact it should be noted that until now only a specific family of exponentials have been used to attempt to model the  $\dot{V}O_2(v, t)$  kinetics; hence it is highly debatable whether the three phases or time delays are needed. We believe that a smooth function of both time and intensity would provide a better model of the physiological processes involved than the three-phase model where the phases turn on and off at discrete time intervals throughout the exercise. We also believe that such a model as the one that we present could be made to fit the raw data for a single exercise bout using the methods that we describe here and that, in fitting it to the data in this form, we can improve our understanding of the underlying physiology.

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**Appendix. Derivation of  $\ddot{V}O_2^k$  from the filtered time series  $[\dot{V}O_2^k]_f$**

The time series  $\ddot{V}O_2^k \equiv \ddot{V}O_2(t^k)$ ,  $k = 0, \dots, N - 1$ , of  $\ddot{V}O_2$  can be numerically derived from the smoothed time series  $[\dot{V}O_2^k]_f$  using a procedure of numerical differentiation, as for example for the three-point formula below which is based on Lagrange polynomial interpolation:

$$\ddot{V}O_2^k = [\dot{V}O_2^{k-1}]_f T^{k-1} + [\dot{V}O_2^k]_f T^k + [\dot{V}O_2^{k+1}]_f T^{k+1} \quad k = 1, \dots, N - 2 \quad (33)$$

where

$$T^{k-1} \equiv \left[ \frac{2t^{k-1} - t^k - t^{k+1}}{(t^{k-1} - t^k)(t^{k-1} - t^{k+1})} \right], \quad k = 1, \dots, N - 2,$$

$$T^k \equiv \left[ \frac{2t^k - t^{k-1} - t^{k+1}}{(t^k - t^{k-1})(t^k - t^{k+1})} \right], \quad k = 1, \dots, N - 2$$

and

$$T^{k+1} \equiv \left[ \frac{2t^{k+1} - t^{k-1} - t^k}{(t^{k+1} - t^{k-1})(t^{k+1} - t^k)} \right], \quad k = 1, \dots, N - 2.$$

It is worth noticing that, in the case of equally spaced sample times (i.e. when  $t^k = t^{k-1} + h = t^{k+1} - h$ ,  $\forall k = 1, \dots, N - 1$ ,  $h \in \mathbb{R}$ ), relation (33) reduces to

$$\ddot{V}O_2^k = \frac{1}{2h} \left[ [\dot{V}O_2^{k+1}]_f - [\dot{V}O_2^{k-1}]_f \right], \quad k = 1, \dots, N - 2. \quad (34)$$

Since the time series  $[\dot{V}O_2^k]_f$  is a smooth curve, the corresponding time series  $\ddot{V}O_2^k$ , calculated as above, will also be smooth.

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