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Empirical modelling of the dynamic response of fatigue during intermittent submaximal contractions of human forearm and calf muscles

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ABSTRACT

Maximum force (F_{max}) declines during intermittent submaximal contractions, but the linearity of this fatigue response and number of underlying phases is not clear. Healthy men were studied during two experiments ($n = 10$ each). Experiment 1 involved single bouts of intermittent forearm contractions (50% F_{max}) to failure using both limbs assigned as $Arm_{control}$ or $Arm_{training}$. Experiment 2 involved five bouts of intermittent calf contractions (60% F_{max}) to failure using the same limb where data from the longest single trial ($Calf_{single}$) or averaged across five bouts ($Calf_{averaged}$) were analysed. F_{max} was assessed at 25–30 s intervals during exercise and fitted to ten mono- and biphasic functions consisting of linear and/or nonlinear terms. For each fatigue response, the function which provided the best fit was determined on statistical grounds. Biphasic functions provided the majority of best fits during $Arm_{control}$ (9/10), $Arm_{training}$ (10/10), $Calf_{single}$ (7/10) and $Calf_{averaged}$ (9/10). For each condition, linear functions provided the best fit in 4–5 out of 10 responses. Two biphasic functions differentiated only by their first term (linear *versus* exponential) provided the best fit for 29/40 fatigue responses. These outcomes suggest that fatigue during intermittent contractions exhibits a biphasic response characterised by nonlinear and linear behaviour.

1. Introduction

Fatigue during exercise is reflected in the progressive loss of maximum force (or power) over time. This response is easily observed during sustained maximum contractions, but it is also apparent during intermittent submaximal contractions when the measurements of maximum force (F_{max}) are interspersed throughout exercise (Fulco et al., 1996). Since fatigue is a time-dependent process, measurement of F_{max} during submaximal exercise has the potential to shed light on the timing and contributions of underlying mechanisms to fatigue (Green et al., 2014).

Inherent in the assessment of fatigue during submaximal exercise is the assumption that fatigue is a monophasic, linear response. This is made explicit when investigators fit temporal responses of F_{max} during exercise to a linear function ($y = a + bx$) and use the slope of this function (b) to assess the rate of fatigue (Egana and Green, 2005, 2007). However, nonlinear behaviour is observed in fatigue responses during submaximal exercise (Egana and Green, 2005), which becomes more apparent at higher intensities (Egana and Green, 2007), and contributes to the curvilinear relationship between exercise intensity and endurance (James and Green, 2012). These observations raise questions about the basic structure of the dynamic response of fatigue, and challenge the assumption that fatigue is a simple linear response.

Empirical modelling has helped elucidate the structure of some physiological responses to exercise (Lamarra, 1990), including oxygen uptake (Lamarra et al., 1987; Barstow and Mole, 1991) and muscle blood flow (Reeder and Green, 2012). Although physiological responses vary between individuals, empirical modelling helps identify the number, size and timing of underlying phases to reveal a response structure common to most individuals (Reeder and Green, 2012). Essential aspects of empirical modelling include the fitting of a single time series of data to two or more algebraic functions, choosing a 'best' function to describe these data, and using statistics to justify this choice (Motulsky and Ransnas, 1987; Lamarra, 1990). Parameters of the best function can be

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linked to one or more phases of the response and provide information about the size, timing or rate at which each phase evolves. These parameters are thought to have physiological meaning and, collectively, empirical modelling provides insight into the timing and contribution of mechanisms underlying the overall response.

To our knowledge, empirical modelling has not been applied to human fatigue responses during submaximal exercise. Therefore, the aim of the present study was to use it to help define the structure of the fatigue response during intermittent, submaximal contractions and address two basic questions. Is fatigue a mono- or biphasic response? Is fatigue a linear or nonlinear response? A narrow range of intensities of submaximal exercise (50–60% F_{max}) was selected to induce substantial fatigue but performed to failure to yield a sufficient number of F_{max} measurements for curve fitting. Fatigue was assessed during forearm and calf contractions to establish whether or not its response varied between muscles of the upper and lower limbs. Finally, we compared outcomes of empirical modelling for data obtained from a single *versus* multiple trials to shed light on recent controversy about this topic (Stirling and Zakynthinaki, 2009; Whipp, 2009).

2. Methods

2.1. Overview

Twenty young, healthy males were studied in two experiments. In Experiment 1, ten subjects (age = 25 ± 7 y; height = 1.81 ± 0.06 m; weight = 76.7 ± 12.7 kg) completed single bouts of intermittent, submaximal forearm contractions using both limbs before commencement of a training program. Limbs were assigned as either a control or a training limb – which was subsequently trained – in a quasi-random manner to ensure an equal distribution of dominant and non-dominant limbs in these groups. In Experiment 2, ten subjects (age = 30 ± 8 y; height = 1.79 ± 0.06 m; weight = 78.2 ± 6.2 kg) completed five bouts of submaximal, intermittent calf contractions on separate days using the same limb. During both experiments, fatigue was represented by the loss of peak force (F_{max}) during exercise, where peak force was measured during brief maximum voluntary efforts interposed between submaximal contractions. Fatigue during forearm contractions was assessed in the control ($Arm_{control}$) and training ($Arm_{training}$) limbs. Fatigue during calf contractions was assessed during the longest of five exercise trials ($Calf_{single}$) and using the averaged F_{max} values from five trials ($Calf_{averaged}$). Both experiments yielded 40 sets of fatigue responses, including 20 datasets from the forearm (Experiment 1) and 20 datasets from the calf (Experiment 2). Each fatigue response was fitted to ten empirical functions, and the function which provided the best fit was determined on statistical grounds. To address the primary research questions, best-fit functions were grouped according to whether they were monophasic or biphasic, as well as linear or nonlinear, and probability testing for a dichotomous variable (1 *versus* 2 phases, linear *versus* nonlinear) was applied. These experiments were conducted in accordance with the Declaration of Helsinki (2008) and approved by the University of the Sunshine Coast Human Research Ethics Committee.

2.2. Forearm exercise (Experiment 1)

Subjects performed single-limb, isometric handgrip exercise while lying supine with the exercising arm abducted to ~90°. Handgrip force was measured using a grip force dynamometer (MLT003/D, AD Instruments, Australia), sampled at 400 Hz (PowerLab 16/30 and Chart v 5.0, AD Instruments) and displayed so that subjects could monitor and control their contractions. Two bouts of exercise were performed by one and then the other arm ($Arm_{control}$ and $Arm_{training}$), separated by 15 min rest, in a randomised order. Prior to each bout, subjects completed five maximum voluntary contractions, separated by 60 s rest, and the highest force was taken as F_{max}. Fifteen minutes later, exercise consisting of intermittent contractions (2 s with 4 s rest) was performed at a target force of 50% F_{max} until it could not be achieved during three consecutive contractions (i.e. task failure). Maximum contractions (2 s duration) were performed 30 s prior to and at 30 s interval throughout exercise, as well as immediately after task failure, for the purpose of describing the fatigue response.

2.3. Calf exercise (Experiment 2)

Calf exercise was performed in the seated position using a custom-built isometric plantar flexion dynamometer. Subjects sat upright with their hip and knee flexed at 90°. A padded knee-plate connected to a calibrated load cell (S1W, Xtran, Applied Measurement, Australia) was clamped over the thigh of the exercising leg and the foot was centred on an immovable footplate. Attempts to plantar flex resulted in the generation of force which was measured and sampled as described for forearm exercise. F_{max} was determined from the highest force achieved during five maximum voluntary contractions separated by 60 s. Fifteen minutes later, exercise consisting of intermittent contractions (2 s with 3 s rest) was performed at a target force of 60% F_{max} until task failure (see Section 2.2). Maximum contractions (2 s duration) were performed 30 s prior to and at 25 s intervals throughout calf exercise, as well as immediately after task failure, again for the purpose of describing the fatigue response as it evolved during exercise. Calf exercise was repeated on five occasions each separated by 7 days.

2.4. Fatigue

Fatigue during exercise is represented by the temporal response of F_{max}. For single trials ($Arm_{control}$, $Arm_{training}$, $Calf_{single}$), the number of F_{max} values used to measure fatigue was a function of the frequency of its measurement and duration of exercise (see Section 3). For $Calf_{averaged}$, F_{max} values were averaged data obtained at the same times during five exercise trials but the duration of each trial varied and a small number (1–4) of measurements were occasionally excluded from analyses for technical reasons. To limit the distortion of averaged data caused by variation in number of observations between trials, the number of F_{max} data used for averaging was limited to 4–5 observations and, consequently, the total number of observations used to assess fatigue during $Calf_{averaged}$ was less than for $Calf_{single}$.

2.5. Functions

Each fatigue response was fitted to ten algebraic functions and graphical representations of these functions are shown in Fig. 1. Functions differed with respect to the number of parameters (2–7), number of phases (1–2), linearity of terms, presence of time delays, and use of conditional arguments. Descriptions of variables, parameters and conditional arguments are provided in Table 1. There are three linear functions, two of which are monophasic (Functions 1, 2) and one which is biphasic (Function 3). There are seven functions containing nonlinear terms and are either monophasic (Functions 4–6) or biphasic (Functions 7–10). Five of these functions contain only nonlinear terms (4, 5, 6, 9 and 10), whereas the remaining two functions (7–8) contain linear and nonlinear terms.