

ORIGINAL ARTICLE

Derek Kay · Frank E. Marino · Jack Cannon
Alan St Clair Gibson · Mike I. Lambert
Timothy D. Noakes

Evidence for neuromuscular fatigue during high-intensity cycling in warm, humid conditions

Accepted: 25 September 2000

Abstract The purpose of this study was to examine and describe the neuromuscular changes associated with fatigue using a self-paced cycling protocol of 60-min duration, under warm, humid conditions. Eleven subjects [mean (SE) age 21.8 (0.8) years; height 174.9 (3.0) cm; body mass 74.8 (2.7) kg; maximum oxygen consumption 50.3 (1.8) ml · kg · min⁻¹] performed one 60-min self-paced cycling time trial punctuated with six 1-min “all out” sprints at 10-min intervals, while 4 subjects repeated the trial for the purpose of determining reproducibility. Power output, integrated electromyographic signal (IEMG), and mean percentile frequency shifts (MPFS) were recorded at the mid-point of each sprint. There were no differences between trials for EMG variables, distance cycled, mean heart rate, and subjective rating of perceived exertion for the subjects who repeated the trial ($n = 4$). The results from the repeated trials suggest that neuromuscular responses to self-paced cycling are reproducible between trials. The mean heart rate for the 11 subjects was 163.6 (0.71) beats · min⁻¹. Values for power output and IEMG expressed as a percentage of that recorded for the initial sprint decreased during sprints 2–5, with normalised values being 94%, 91%, 87% and 87%, respectively, and 71%, 71%, 73%, and 77%, respectively. However, during the final sprint normalised power output and IEMG increased to 94% and 90% of initial values, respectively. MPFS displayed an increase with time; however, this was not significant ($P = 0.06$). The main finding of this investigation is the ability of subjects

to return power output to near initial values during the final of six maximal effort sprints that were included as part of a self-paced cycling protocol. This appears to be due to a combination of changes in neuromuscular recruitment, central or peripheral control systems, or the EMG signal itself. Further investigations in which changes in multiple physiological systems are assessed systematically are required so that the underlying mechanisms related to the development of fatigue during normal dynamic movements such as cycling can be more clearly delineated.

Key words Integrated electromyographic signal · Fatigue · Temperature · Self-paced cycling · Power

Introduction

The ease with which trained athletes perform masks the complex interactions between the physiological systems involved. Successful performance relies on the maintenance of neuromuscular function; however, factors such as temperature may interfere with such control systems and their function (Montgomery and MacDonald 1990). The most notable modification to the neuromuscular system during exercise is the development of fatigue. Although a common experience, a century of investigation has been unable to completely elucidate a common physiological basis for this phenomenon, as the complexity of the neuromuscular system does not facilitate the evaluation of all of the events that occur during fatigue development. Electromyography (EMG) allows for one aspect of the neuromuscular system to be assessed, that of motor unit pool activation patterns (Viitasalo and Komi 1977). While the measurement of myoelectric activity is a classical approach to investigating the motor control of human movement, multiple factors other than fatigue may induce changes in this variable (Oska et al. 1996).

D. Kay · F. E. Marino (✉) · J. Cannon
Human Movement Studies Unit and Human Performance
Laboratory, Charles Sturt University,
Bathurst NSW 2795, Australia
e-mail: fmarino@csu.edu.au
Tel.: +61-2-63384268; Fax: +61-2-63384065

A. St Clair Gibson · M. I. Lambert · T. D. Noakes
MRC/UCT Bioenergetics of Exercise Research Unit,
Department of Physiology, University of Cape Town Medical
School, Cape Town, South Africa

Central to the study of fatigue is the definition that is employed. In general, fatigue is viewed as an unavoidable and negative consequence of physical activity, since the outcome almost exclusively results in reduced performance and function (Kirkendall 1990). However, such a view limits the understanding of this phenomenon. It may be more appropriate to view fatigue as a safety mechanism, modulated by either central or peripheral input, preventing metabolic crisis and preserving the integrity of the muscle fibre (Sargeant 1994), thus preventing the development of injury or death by forcing a reduction in the intensity or cessation of activity (Noakes 1998; Wagenmakers 1992). As suggested previously (Kay and Marino 2000), fatigue should be viewed as a continuous process that transforms the functional state, with exhaustion being the point at which exercise is terminated.

Traditionally, submaximal endurance exercise has been used to assess and infer a level of "fatigue". Such protocols do not facilitate the systematic study of muscle fatigue, since no provision is made for the periodic assessment of muscle force/power output, permitting only a "snapshot" of the physiological events associated with muscular exhaustion (Lewis and Fulco 1998). Alternatively, it may be possible to quantify muscle fatigue following dynamic movements such as running and cycling by performing static contractions at the completion of exercise. However, this may not allow for adequate crossover between the musculature used to develop the fatigue and those used to assess it. Moreover, the inevitable delay in assessment would result in a partial recovery of force production capacity (Lewis and Fulco 1998). Furthermore, the results of previous investigations suggest that fatigue development is activity and contraction-type specific (Enoka and Stuart 1992; Kay et al. 2000; Tesch et al. 1990). Studies by Nielsen et al. (1993) and Gonzalez-Alonso et al. (1999) indicate that a potential limiting factor for human performance is the capacity to store heat. The conditions of elevated temperature and humidity reduce the capacity of the body to dissipate heat to the environment, thus increasing the internal thermal load. According to the model presented by these authors, environmental thermal stress would increase heat storage, thus prematurely developing fatigue during exercise.

With such specificity in the factors associated with the onset of fatigue it seems appropriate, if not essential,

that data describing the development of fatigue be obtained from the performance of specific activities. It is recommended that the investigation of muscle function take place during normal movements where numerous factors combine to complicate the application and interpretation of the resultant neuromuscular patterns (Sargeant 1987). In response to the paucity of data describing the development of fatigue under dynamic conditions, this study was undertaken to examine and describe the neuromuscular events associated with fatigue using a self-paced cycling protocol of 60-min duration, under elevated environmental conditions.

Methods

Subjects and experimental design

Eleven subjects (8 men, 3 women) were recruited for the study. All were physically active, and were familiar with cycling exercise and the performance of intense physical activity for extended periods. The mean physical characteristics of the subjects are given in Table 1. The study was conducted with the approval of the Ethics in Human Research Committee of the University, and each subject signed a letter of informed consent. Initially all subjects completed an incremental test to exhaustion. This was followed by a familiarisation session 7 days later, which incorporated the self-paced cycling protocol to be undertaken in the experimental trials under similar experimental and environmental conditions.

Seven to 14 days after all subjects had completed the incremental test and familiarisation session, all subjects completed at least one experimental trial. In order to assess the reproducibility of neuromuscular responses to exercise of this nature, 4 of the 11 subjects repeated the trial at least 5 days following the initial experimental trial.

Peak power determination

During this session of the study, descriptive data were collected and all subjects underwent a progressive incremental test to exhaustion for the determination of peak power output and peak oxygen consumption ($\dot{V}O_{2\text{peak}}$). Subjects performed this test using his or her own bicycle, which was mounted onto an electromagnetic trainer (Tacx, Technische Industrie Tacx, Wassenaar, The Netherlands). Following a brief warm-up at a self-selected intensity, the test commenced at a workload of 100 W. The load was then increased by 10 W at 30-s intervals until the required power output could no longer be maintained. At all times throughout the test subjects were required to remain in a seated position.

During the maximal test, subjects breathed through a two-way non-rebreathing valve (series 2700 large, Hans Rudolph, St. Louis, Mo., USA), using respiratory tubing of 2.74 m length and 3.5 cm diameter (Hans Rudolph). Expired air passed via the respiratory

Table 1 Data are given as the means, standard error of the mean (SE) and range for physical characteristics and peak physiological variables for 11 subjects (8 males, 3 females). (*ΣSF* Sum of skinfolds, f_{cmax} maximum heart rate achieved during incremental power tests, $\dot{V}O_{2\text{peak}}$ peak oxygen consumption)

Parameter	Age (years)	Height (cm)	Mass (kg)	ΣSF (mm)	$\dot{V}O_{2\text{peak}}$ (ml · kg · min ⁻¹)	f_{cmax} (beats · min ⁻¹)	Peak power (W)	Mean power output (W)	Total distance cycled (km)
Mean	21.8	174.9	74.8	109.0	50.3	186.2	285.6	215.1	29.06
Range	18–26	164–197	57.2–86.0	62.0–211.0	37.7–58.3	169–202	220–310	131–297	20.1–36.0
SE	0.8	3.0	2.7	17.2	1.8	2.8	11.3	14.8	1.5

tubing to an automated gas analyser (Quinton Instrument Company, Bothell, Wash, USA). The pneumotach (Hans Rudolph) and gas analysers were calibrated prior to analysis, using a 3-l syringe and gasses of known concentration. Expired air passed through a mixing chamber of 5.5-l volume and subsequently sampled at 30-s intervals.

Performance trial

The performance trial required participants to undertake a 60-min self-paced cycling time trial, with the primary goal to complete the greatest distance possible within the allotted time. Throughout the trials the average temperature and humidity was 33 ± 0.3 °C and $64 \pm 0.2\%$, respectively. Trials were performed with subjects using their own bicycle, which was mounted onto the electromagnetic cycle trainer that was used in the peak power tests. During the trial subjects were allowed to alter the gear ratio and pedalling cadence as required. In an attempt to represent the stochastic nature of cycle racing and to provide an additional measure of performance, six 1-min "all out" sprints were included in the performance trial. Sprints were scheduled during the 10th, 20th, 30th, 40th, 50th, and 60th min of the trial. Subjects were encouraged to perform a maximal effort for the entire duration of the sprint. Throughout all sprint intervals subjects were required to remain in a seated position to prevent alterations in muscle fibre recruitment patterns that result from changes in posture. The intra-class correlation for distance cycled for this protocol has been previously determined to be 0.93. Furthermore, the within-cyclist coefficient of variation (CV) following the completion of at least one familiarisation trial for this protocol is 1.34% (Marino et al., unpublished observations).

Participants were instructed to complete the greatest distance possible in the allowed time, taking into consideration the sprints. Prior to each sprint the investigator gave subjects a time count leading up to the commencement of the sprint. During the trial subjects viewed a course profile indicating where sprints occurred, and were permitted to monitor elapsed time and heart rate (f_c). Power output (W) and distance (km) were monitored throughout each experiment and were recorded at 5-min intervals. During all trials, a fan providing a constant wind speed of $3 \text{ m} \cdot \text{s}^{-1}$ was placed directly in front of the subject and positioned so that the airflow was directed towards the head and torso when in a normal cycling position. Throughout the cycling trials fluid (water) was available to the participants ad libitum to a maximum of 200 ml.

Subjects were requested to perform the same type of physical activity for the duration of the study and to refrain from heavy physical exercise on the day prior to the time trial. Participants were requested to standardise their fluid and food intake for the day preceding the trial, as well as for the day of the time trial. In addition, subjects were required to abstain from the ingestion of alcohol, caffeine, and tobacco for 24 h prior to each trial.

Neuromuscular measurements

Prior to exercise, EMG electrodes with a bandwidth of 20–450 Hz were attached to the "belly" of the rectus femoris muscle. The skin overlying these muscles was carefully prepared. Hair was shaved off, the outer layer of epidermal cells abraded, and oil and dirt were removed from the skin with an alcohol swab. Differential surface electrodes (Delsys, Boston, Mass., USA) were placed on the muscle site as described above, and linked via insulated cable to the signal acquisition apparatus (Bagnoli 4, Delsys) and host computer, which was equipped with data acquisition software (Delsys). EMG data were sampled at 1024 Hz during all tests, thus yielding raw signals; no notch filter was applied. The EMG electrodes consisted of a parallel bar configuration with an inter-electrode distance of 10 mm. The reference electrode consisted of a gel adhesive electrode. The site for the reference electrode was prepared as described above and positioned over an electrically neutral and mechanically stable site.

Raw EMG signals were full-wave rectified. The movement artefact was removed using a high-pass second order Butterworth filter with a cut-off frequency of 15 Hz, then the signal was smoothed with a low-pass second-order Butterworth filter with a cut-off frequency of 5 Hz. This was performed using MATLAB gait analysis software. Commencing at the midpoint of each of the six sprints, 5 s of EMG data were obtained. The mean EMG activity for each 5-s interval was then calculated. The data collected during the initial sprint is described as 100% EMG activity; while all subsequent data were normalised by using this value as the denominator in Eq. 1:

$$\text{Sprint } (x) \text{ value} = \text{absolute value } x \text{ (Volts)/sprint 1 value} \times 100 \quad (1)$$

where x represents sprints 2–6 to be compared with the values from sprint 1. All subsequent sprints were normalised with respect to time against the value obtained in the initial sprint. Corresponding data for power output was normalised with respect to time using the above procedure.

The frequency spectrum of each epoch of the raw EMG data was analysed using a fast Fourier transformation algorithm. The frequency spectrum analysis was restricted to frequencies in the range 5–500 Hz, as the EMG signal content outside of this range consists mostly of noise. The frequency spectrum from each epoch of data was compared with that from the first epoch, and the amount of spectral compression was estimated. This was performed using the technique described by Lowery et al. (1998), as a modification of the work of Lo Conte and Merletti (1996) and Merletti and Lo Conte (1997). The spectrum of the raw signal of each epoch was obtained and the normalised cumulative power at each frequency was calculated. The shift in each percentile frequency (i.e. at 0%...50%...100% of the total cumulative) was examined. The frequency shift was then estimated by calculating the mean shift in all percentile frequencies (MPFS) throughout the mid-frequency range (i.e. 5–500 Hz). It has been suggested that this method is a more accurate estimate of spectral compression than median frequency analysis, which uses the value of a single (50th) percentile frequency only (Lo Conte and Merletti 1996; Lowery et al. 1998; Merletti and Lo Conte 1997).

f_c and rating of perceived exertion

f_c was recorded during all sessions using an f_c monitor and transmitter strap (Vantage NV, Polar Electro Oy, Kempele, Finland). Maximal f_c was determined as the maximum f_c recorded during the peak power test. f_c data were recorded at 15-s intervals and transferred to computer for subsequent analysis. Subjective ratings of perceived exertion (RPE; Borg 1982) were also recorded at 5-min intervals during each trial.

Body temperatures and sweating

Nude body mass was measured to the nearest 10 g prior to and following each cycling trial, using an electronic precision balance (HW-100KAI, GEC, Avery, Australia). The difference in body mass was then used to determine total body sweating ($l \cdot h^{-1}$) after correcting for fluid ingestion. For the four subjects who repeated the experimental trials, the changes in core temperature were monitored using a tympanic thermometer (IRT 1020, Thermoscan, San Diego, Calif., USA) for ethical and safety reasons and as an indicator of thermal strain between trials. It was thought that a more invasive procedure such as oesophageal or rectal probe might have interfered with the performance of subjects. However, after assessing the responses to these trials and determining that there were no significant physiological differences between trials, the remaining seven subjects had core temperature monitored via a rectal thermistor (Mono-a-therm, Mallinckrodt Medical, St. Louis, Mo., USA), which was inserted 10 cm beyond the anal sphincter and connected to a telethermometer (Zencor, Australia).

Descriptive statistics were generated for all data. The data for the repeated trials ($n = 4$) were analysed by repeated-measures (trial \times time) analysis of variance (ANOVA), and no statistical differences were detected. Therefore, a within-subject one-way repeated-measures ANOVA for time was used to analyse the data for the entire group ($n = 11$). To avoid violation of the homogeneity of variance assumption, the Huynh-Feldt correction factor was used to adjust the degrees of freedom associated with each of the separate repeated-measures analysis. Once the main effects were identified, individual differences between means were located using Tukey's HSD post hoc procedure. The CV was determined from the mean value of individual calculations. Paired samples t -tests were used where appropriate. Significance was accepted at $P < 0.05$. All data are presented as the means (SE).

Results

The mean values for $\dot{V}O_{2\text{peak}}$, peak power output, power output and distance cycled during the 60-min trial are given in Table 1. The four subjects who repeated the trials showed no differences between trials for total distance cycled [26.63 (2.25) km vs 28.80 (2.25) km; $P = 0.28$]. Similarly, there were no differences between trials for f_c ($P = 0.66$) and RPE ($P = 0.93$), with mean values being 170 (1) and 170 (1) beats \cdot min $^{-1}$, and 14 (2) and 13 (1), respectively, for trials 1 and 2, respectively. For both trials, the starting tympanic temperature was ≈ 36.4 $^{\circ}\text{C}$, and this had increased to ≈ 37.9 $^{\circ}\text{C}$ ($\Delta 1.4$ $^{\circ}\text{C}$; $P < 0.05$) by the end of exercise. There were no differences between trials for normalised power output ($P = 0.71$), integrated EMG (IEMG; $P = 0.35$), and MPFS ($P = 0.90$) during any of the sprint intervals (Fig. 1). During both trials, normalised IEMG values were significantly decreased for all sprint intervals following the initial sprint ($P < 0.05$). For each of the repeated trials normalised power output displayed a similar pattern in tracking normalised IEMG responses (Fig. 1). The CV for IEMG, power output, and MPFS for the repeated trials were 16.1%, 4.3%, and 1.9%, respectively. Previous studies reporting the test-retest reliability of EMG variables have described similar results (Taylor and Bronks 1995).

f_c and RPE for the eleven subjects are shown in Fig. 2. The mean f_c for the entire trial was 163.6 (0.71) beats \cdot min $^{-1}$, with mean values attained during sprints 1–6 being 171 (4.3), 177 (4.2), 178 (5.0), 179 (4.3), 182 (3.8), and 183 (4.2) beats \cdot min $^{-1}$, respectively. The starting rectal temperature was 37.5 (0.1) $^{\circ}\text{C}$, and this had increased to 38.9 (0.2) $^{\circ}\text{C}$ ($P < 0.05$; $\Delta 1.4$ $^{\circ}\text{C}$; $n = 7$) by the end of exercise. The mean total body sweat rate was 1.49 (0.15) l \cdot h $^{-1}$. Subjective ratings of RPE over time are presented in Fig. 2, with the mean RPE for the trial being 13.6 (1.0).

Normalised power output, IEMG, and MPFS for all eleven subjects are shown in Fig. 3. Values for power output expressed as a percentage of initial sprint power decreased with respect to time, reaching significance during sprints 4 and 5 ($P = 0.05$). Values for power

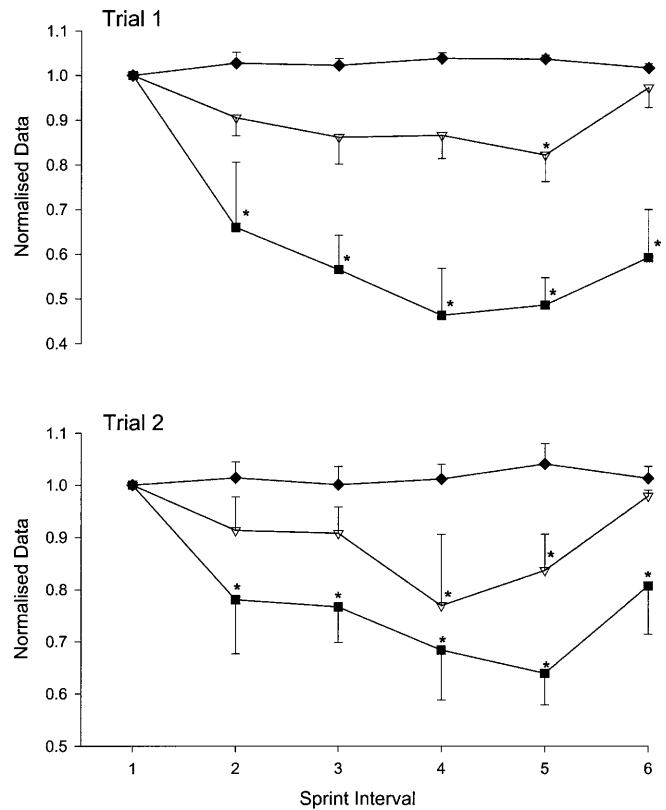


Fig. 1 Time-normalised data for power output (open triangles), integrated electromyogram (IEMG; closed squares), and frequency spectrum (closed diamonds) during trials 1 and 2, collected at the mid-point of each of the sprints during a 60-min cycling trial conducted under warm, humid conditions. Data are presented as the means \pm SE ($n = 4$). * $P < 0.05$, significant compared with first time point

output expressed as a percentage of initial sprint decreased during sprints 2–5, with normalised values being 94%, 91%, 87% and 87%, respectively. Similarly, normalised IEMG values for the same sprints were 71%, 71%, 73%, and 77% of initial values, respectively. However, during the final sprint, normalised power output and IEMG recovered to 94% and 90% of initial values, respectively. MPFS increased with time; however, this increase was not significant ($P = 0.06$). A representative sample of IEMG data obtained from one subject during each sprint interval is presented in Fig. 4.

Discussion

This study describes the efferent neural output of the rectus femoris muscle during high-intensity sprints that were included in a 60-min self-paced cycling protocol. The results of the present study demonstrate a reduction in efferent drive and power output commencing in the early stages of exercise. However, this initial reduction in efferent drive, observable in sprints 2–4, was accompanied by an increasing efferent output to the

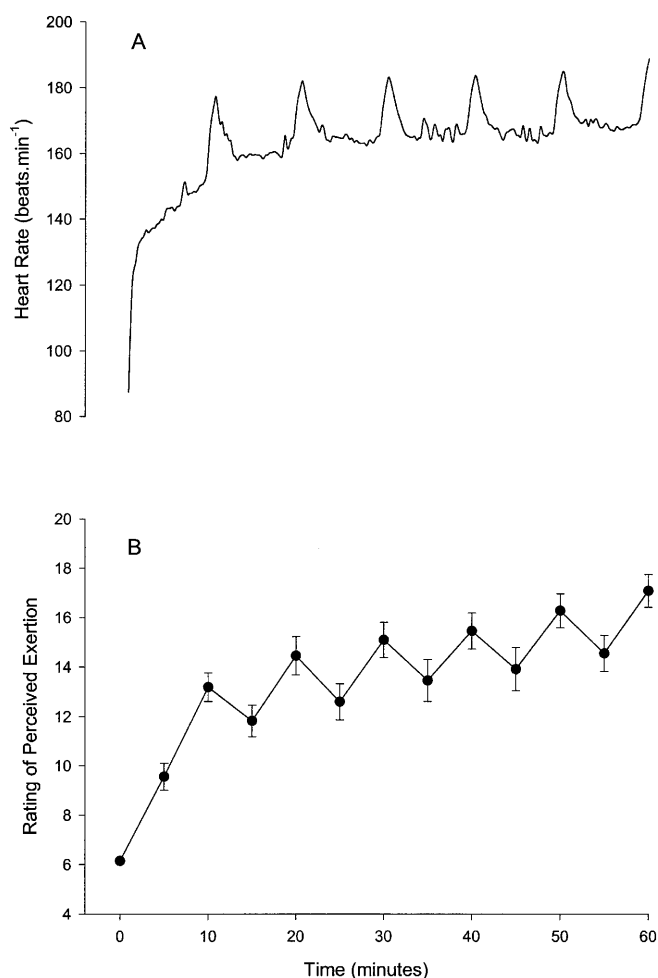


Fig. 2 Mean heart rate at 15-s intervals **A** and rating of perceived exertion **B** during the 60-min self-paced cycling time trial. Data are presented as the means \pm SE ($n = 11$)

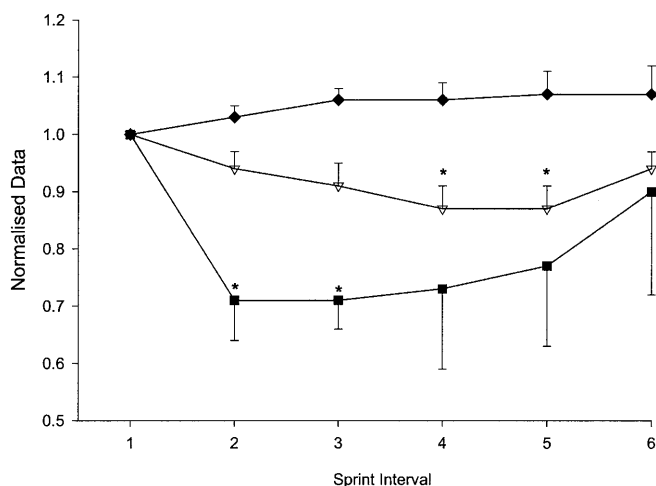


Fig. 3 Time normalised data for power output (open triangles), IEMG (closed squares), and frequency spectrum (closed diamonds) collected at the mid-point of each of the sprints during a 60-min cycling trial conducted under warm, humid conditions. Data are presented as the means \pm SE ($n = 11$). * $P < 0.05$, significant compared with first time point

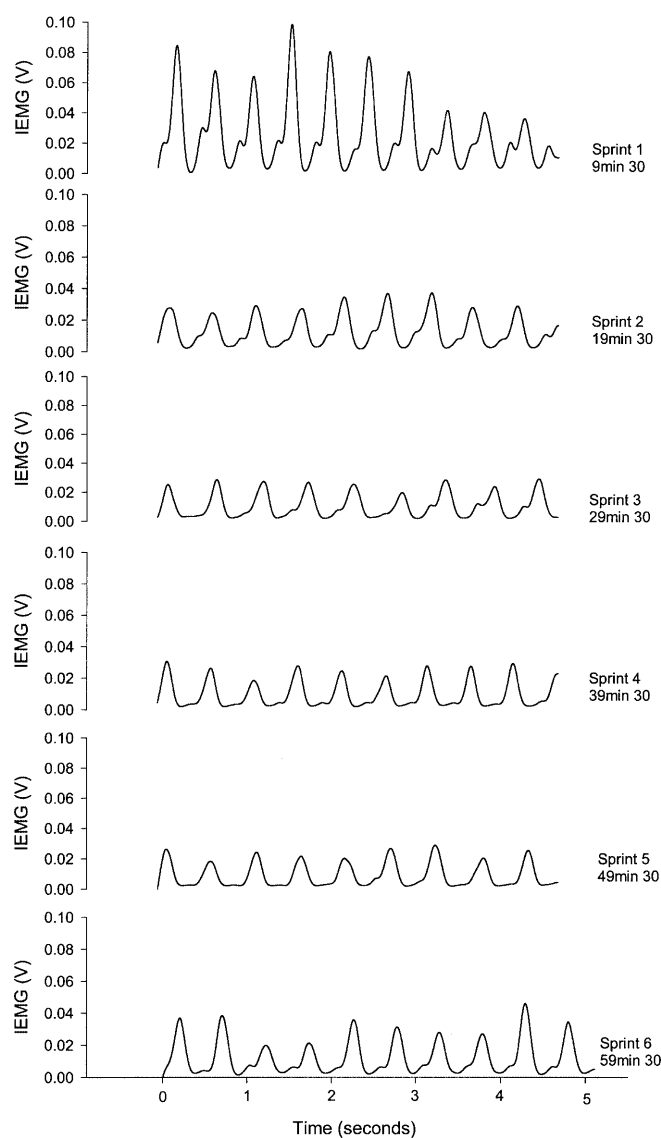


Fig. 4 Representative IEMG data for one subject. Data were collected at the mid-point of each of the sprints during a 60-min cycling trial conducted under warm, humid conditions

active muscle during the concluding stages of exercise (sprint 6), resulting in a concomitant increase in power output. This suggests the existence of a subconscious muscle reserve during the initial five sprints, despite a conscious effort by all subjects, as evidenced by the similar f_c and RPE response prior to and following each sprint. A secondary finding of the present investigation is that this neuromuscular response pattern to stochastic self-paced exercise is reproducible between trials (Fig. 3).

The results of the present study show that during the final minute of a 60-min self-paced cycling protocol where subjects were required to produce a maximal effort, it was possible to restore power output to near initial values. This restoration of power output during the final sprint was accompanied by a similar increase in

the IEMG signal of the rectus femoris muscle (Fig. 3). Subjects were clearly able to increase the neural drive to the muscle in conjunction with an increasing power output during the final sprint, suggesting not only maintenance of the ability to activate the muscle, but the presence of a neuromuscular reserve during self-paced exercise. This occurred despite subjects being required to perform a maximal effort for the entire duration of each sprint interval.

Migration of motor unit activity to synergist muscles may have allowed for the maintenance of force output relative to the observed IEMG of the rectus femoris (Komi and Tesch 1979). However, we were unable to determine the degree with which the activation of synergist muscles contributed to the power output during this study. Previous investigations have shown recruitment patterns to be altered with fatiguing activity (Bangsbo et al. 1992; Nicol et al. 1991; Nummela et al. 1992). It remains possible that lower limb inter-muscular recruitment strategies were altered as subjects fatigued, with other muscles being recruited at different levels to the single muscle measured in this study. However, investigation by Sacco et al. (1997) suggests that fatigue of one muscle is closely associated with fatigue of synergistic muscles. The finding that the reduction in IEMG activity was mirrored by power output suggests that the synergistic muscles involved in cycling activity display a similar pattern to that of the rectus femoris and were not recruited to compensate for the falling power output or reduced efferent drive to this muscle.

It has been suggested that alterations in excitation/contraction coupling or the contractile apparatus (Bangsbo et al. 1992; Häkkinen and Komi 1983) are the factors that are responsible for the reduction in power output observed during fatiguing activity. However, throughout all sprints a regular cycling EMG pattern was maintained (Fig. 4), indicating that impairment of the excitation/coupling mechanism is unlikely to be the cause of the attenuated efferent signal observed in the present study. If this mechanism was responsible it would result in the cessation of cycling exercise. In addition to the progressive reduction in amplitude, a feature of Fig. 4 is the double peak that occurs prominently during muscle activation throughout the initial sprint. This is a result of the rectus femoris muscle being active in conjunction with the extensor muscles, assisting with flexion of the hip during the recovery phase of the pedalling motion (Burke 1995). Activation of the rectus femoris during the recovery phase is clearly distinguishable from the propulsive phase during the initial sprint. However, by the fifth sprint this component of the pedal cycle can no longer be observed. During the final sprint, although distinguishable, this component of the pedal cycle remains irregular compared to that observed during the initial sprint. Although qualitative, these data indicate an alteration in the coordination pattern of the cycling movement in conjunction with the development of fatigue.

Rectal temperature increased progressively during the cycling trial, resulting in terminal values of ≈ 38.9 °C. The relationship between the core temperature and muscle temperature (T_m) response during physical activity appears to be proportional (Kozlowski et al. 1985). Since all neural processes are temperature sensitive (Montgomery and MacDonald 1990), changes in T_m induced either by environmental conditions or physical activity have the potential to alter the contractile and metabolic properties of muscle fibres, in turn impacting on the capacity to sustain work output (Sargeant 1994).

Increases in T_m have been associated with increases in peak muscle force (Davies and Young 1983; Sargeant 1987), due to temperature-induced alterations in neuromuscular recruitment patterns (Holewijn and Heus 1992), increased conduction velocity and contractile speed (Bell 1993; Davies and Young 1983; Sargeant 1987; Zhou et al. 1998), and the earlier and more pronounced development of muscle fatigue (Holewijn and Heus 1992), suggesting failure of the fatigue-susceptible fast-twitch fibres. However, since we did not measure T_m , it is not possible to fully relate EMG responses to changes in this variable. Furthermore, the EMG signal may be influenced by alteration in the fluid content of the muscle (Winkle and Jørgensen 1991) and the additional perspiration generated by prolonged activity (Bell 1993), particularly under conditions of elevated temperature.

The data from the present study indicate that during 60 min of continuous cycling activity under elevated environmental conditions, power output was tracking IEMG activity (Figs. 1, 3). This finding suggests that the observed attenuation in IEMG activity during the initial stages of the trial may not be a function of changes in temperature, conductivity, or electrode placement. With the continuation of exercise and the development of fatigue, progressive decreases in the frequency content of the active muscle could be expected (Viitasalo and Komi 1977). In contrast, the present results demonstrate the maintenance of MPFS during exercise. It is possible that this resulted from either increasing core temperature and T_m , or changes in recruitment strategy, with the selective recruitment of type II fibres occurring towards the end of the trial (Basmajian and DeLuca 1985).

Finally, the protocol utilised in the present study was self-paced; thus subjects were aware of the duration of the trial and the number of sprints to be performed. Ulmer (1996) suggested that efferent command signals to muscles not only regulate the spatial and temporal pattern of motion, but also act to control metabolic rate. This suggestion includes the presence of a central control that acts to balance the requirements of the activity with metabolic changes within the body. This system would act to allow the individual to most efficiently complete the activity without the development of physiological damage or premature fatigue. The present results give support to the existence of such a mechanism through the decreasing power output and efferent command to the active muscle during the initial sprint intervals, despite a similar physiological effort during the trial, as

evidenced by f_c and RPE values prior to and immediately following the sprints.

In summary, this investigation has described the neuromuscular and performance changes that occur during self-paced cycling. Further investigations in which the changes in multiple physiological systems are assessed systematically are required so that the underlying mechanisms responsible for the development of fatigue during normal dynamic movements such as cycling can be more clearly described.

Acknowledgements The authors would like to thank the participants for their enthusiastic participation throughout the study. F.E. Marino and D. Kay were supported by a CSU small grant and a CSU postgraduate research studentship. T.D. Noakes, M.I. Lambert, and A. St Clair Gibson were supported by the Harry Crossley Research Fund of the University of Cape Town, and the Medical Research Council of South Africa.

References

- Bangsbo J, Graham TE, Keins B, Saltin B (1992) Elevated muscle glycogen and aerobic energy production during exhaustive exercise. *J Physiol (Lond)* 451: 205–227
- Basmajian JV, DeLuca CJ (1985) *Muscles alive, their function revealed by electromyography*. Williams and Wilkins, Baltimore
- Bell DG (1993) The influence of air temperature on the EMG/force relationship of the quadriceps. *Eur J Appl Physiol* 67: 256–260
- Borg GAV (1982) Psychological bases of physical exertion. *Med Sci Sports Exerc* 14: 377–381
- Burke ER (1995) *Serious cycling*. Human Kinetics, Champaign, Ill
- Davies CTM, Young K (1983) Effect of temperature on the contractile properties and muscle power of triceps surae in humans. *J Appl Physiol* 55: 191–195
- Enoka RM, Stuart DG (1992) Neurobiology of muscle fatigue. *J Appl Physiol* 72: 1631–1648
- González-Alonso J, Teller C, Andersen SL, Jensen FB, Hyldig T, Nielsen B (1999) Influence of body temperature on the development of fatigue during prolonged exercise in the heat. *J Appl Physiol* 86: 1032–1039
- Hagberg M (1981) Muscular endurance and surface electromyogram in isometric and dynamic exercise. *J Appl Physiol* 51: 1–7
- Häkkinen K, Komi PV (1983) Electromyographic and mechanical characteristics of human skeletal muscle fatigue under voluntary and reflex conditions. *Electroencephalogr Clin Neurophysiol* 55: 436–444
- Holewijn M, Heus R (1992) Effects of temperature on electromyogram and muscle function. *Eur J Appl Physiol* 65: 541–545
- Kay D, Marino FE (2000) Fluid ingestion and exercise hyperthermia: implications for performance, thermoregulation, metabolism, and the development of fatigue. *J Sport Sci* 18: 71–82
- Kay D, St Clair Gibson A, Mitchell M, Lambert MI, Noakes TD (2000) Different neuromuscular recruitment patterns during eccentric, concentric, and isometric contractions. *J Electromyogr Kinesiol* (in press)
- Kirkendall DT (1990) Mechanisms of peripheral fatigue. *Med Sci Sports Exerc* 22: 444–449
- Komi PV, Tesch P (1979) EMG frequency spectrum, muscle structure, and fatigue during dynamic contractions in man. *Eur J Appl Physiol* 41: 41–50
- Kozlowski S, Brzezinska Z, Kruk B, Kaciuba-Uscilko H, Greenleaf JE, Nazar K (1985) Exercise hyperthermia as a factor limiting physical performance: temperature effect on muscle metabolism. *J Appl Physiol* 59: 766–773
- Lewis SF, Fulco CS (1998) A new approach to studying muscle fatigue and factors affecting performance during dynamic exercise in humans. In: Holloszy J (ed) *Exercise and sport science reviews*. Williams and Wilkins, Baltimore, pp 91–117
- Lo Conte LR, Merletti R (1996) Estimating EMG spectral compression: comparison of four indices. 18th Annual International Conference of the IEEE, 30th Oct–2nd Nov, Amsterdam, The Netherlands. Institute of Electrical and Electronic Engineers, Piscataway, N.J., USA, pp 2–5
- Lowery M, O'Malley M, Vaughan C, St Clair Gibson A (1998) A physiologically based simulation of the electromyographic signal. In: Arsenault AB, McKinley P, McFadyen B (eds) *Proceedings of the 12th International Society of Electrophysiology and Kinesiology*, June 27–30, Montreal, Canada. Elsevier Science, Oxford
- Merletti R, Lo Conte LR (1997) Surface EMG signal processing during isometric contractions. *J Electromyogr Kinesiol* 7: 241–250
- Montgomery JC, MacDonald JA (1990) Effects of temperature on nervous system: implications for behavioural performance. *Am J Physiol* 259: R191–R196
- Nicol C, Komi PV, Marconnet P (1991) Fatigue effects of marathon running on neuromuscular performance. *Scand J Med Sci Sports* 1: 18–24
- Nielsen B, Hales JRS, Strange S, Christensen NJ, Warberg J, Saltin B (1993) Human circulatory and thermoregulatory adaptations with heat acclimation and exercise in a hot, dry environment. *J Physiol (Lond)* 460: 476–485
- Noakes TD (1998) Maximal oxygen uptake: “classical” versus “contemporary” viewpoints: a rebuttal. *Med Sci Sports Exerc* 30: 1381–1398
- Nummela A, Vuorimaa T, Rusko H (1992) Changes in force production, blood lactate and EMG activity in the 400-m sprint. *J Sports Sci* 10: 217–228
- Oska J, Rintamäki H, Mäkinen T, Martikkala V, Rusko H (1996) EMG-activity and muscular performance of lower leg during stretch-shortening cycle after cooling. *Acta Physiol Scand* 157: 71–78
- Sacco P, Newberry R, McFadden L, Brown T, McComas AJ (1997) Depression of human electromyographic activity by fatigue in a synergistic muscle. *Muscle Nerve* 7: 710–717
- Sargeant AJ (1987) Effect of Tm on leg extension force and short term power output in humans. *Eur J Appl Physiol* 56: 693–698
- Sargeant AJ (1994) Human power output and muscle fatigue. *Int J Sports Med* 15: 116–121
- Taylor AD, Bronks R (1995) Reproducibility and validity of the quadriceps muscle integrated electromyogram threshold during incremental cycle ergometry. *Eur J Appl Physiol* 70: 252–257
- Tesch PA, Dudley GA, Duvoisin MR, Hather BM, Harris RT (1990) Force and EMG signal patterns during repeated bouts of concentric or eccentric muscle actions. *Acta Physiol Scand* 138: 263–271
- Ulmer HV (1996) Concept of an extracellular regulation of muscular metabolic rate during heavy exercise in humans by psychophysiological feedback. *Experientia* 52: 416–420
- Viitasalo JHT, Komi PV (1977) Signal characteristics of EMG during fatigue. *Eur J Appl Physiol* 37: 111–121
- Wagenmakers AJ (1992) Role of amino acids and ammonia in mechanisms of fatigue. In: Marconnet P, Komi PV, Saltin B, Sejersted OM (eds) *Muscle fatigue mechanisms in exercise and training*. *Med Sport Sci* 34: 69–86
- Winkle J, Jørgensen K (1991) Significance of skin temperature changes in surface electromyography. *Eur J Appl Physiol* 63: 345–348
- Zhou S, Carey MF, Snow RJ, Lawson DL, Morrison WE (1998) Effects of fatigue and temperature on electromechanical delay. *Electromyogr Clin Neurophysiol* 38: 67–73