Prior heavy exercise increases oxygen cost during moderate exercise without associated change in surface EMG

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Abstract

The aim of this study was to test the hypothesis that prior heavy exercise results in a higher oxygen cost during a subsequent bout of moderate exercise due to changes in muscle activity. Eight male subjects (25 ± 2 yr, $\pm SE$) performed moderate–moderate and moderate–heavy–moderate transitions in work rate (cycling intensity, moderate $= 90\%$ LT, heavy $= 80\%$ $\dot{V}O_2$ peak). The second bout of moderate exercise was performed after 6 min (C) or 30 s (D) of recovery. Pulmonary gas exchange was measured breath-by-breath and surface electromyography was obtained from the vastus lateralis and medialis muscles. Root mean square (RMS) and median power frequency (MDPF) were computed. Prior heavy exercise increased $\Delta\dot{V}O_2/\Delta WR$ (C: $+2.0 \pm 0.8$ ml min^{-1} W^{-1}, D: $+3.4 \pm 0.8$ ml min^{-1} W^{-1}; $P < 0.05$) and decreased exercise efficiency (C: $-13.3 \pm 5.6\%$, D: $-22.2 \pm 4.9\%$; $P < 0.05$) during the second bout of moderate exercise in the absence of changes in RMS. MDPF was slightly elevated ($\sim2\%$) during the second bout of moderate exercise, but MDPF was not correlated with $\dot{V}O_2$ ($r = 0.17$). These findings suggest that the increased oxygen cost during moderate exercise following heavy exercise is not due to increased muscle activity as assessed by surface electromyography.

1. Introduction

During the adjustment to an abrupt increase in exercise intensity, pulmonary oxygen uptake ($\dot{V}O_2$) increases, after a short delay, towards a new steady-state if the exercise is of moderate intensity (i.e. below the lactate threshold, LT). Results from a number of studies (Barstow and Molé, 1991; Barstow et al., 1993) suggest that the characteristics of the $\dot{V}O_2$–work rate relationship during moderate exercise can be described as a linear dynamic system, that is with an invariant time constant and a proportional change in ampli-

tude for a given increase in work rate. Typically, the gain ($\Delta\dot{V}O_2/\Delta WR$) of the $\dot{V}O_2$–work rate relationship, whether determined during ramp or constant work rate exercise, approximates 10 ml min^{-1} · W^{-1} except for heavy exercise where $\Delta\dot{V}O_2/\Delta WR$ may approach $\geqslant 12$ ml min^{-1} · W^{-1} (Barstow et al., 1993; Henson et al., 1989; Roston et al., 1987). Through the noninvasive examination of muscle activity by surface electromyography (sEMG), Bigland-Ritchie and Woods (1974) has shown that $\dot{V}O_2$ increases in linear fashion with increases in force and motor unit recruitment, a finding that has since been confirmed by other studies (Hug et al., 2004; Jammes et al., 1998). The recruitment of motor units for the production of force couples skeletal muscle activity to the metabolic rate (as $\dot{V}O_2$) during physical exercise as energy is required for muscular contraction.

Since Gerbino et al. (1996) first reported that a prior bout of heavy exercise resulted in a speeding of the mean response time of $\dot{V}O_2$ kinetics during a subsequent bout

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of heavy exercise, several investigators have manipulated this protocol in an effort to identify the factor(s) that regulate both the rate of adjustment and amplitude of the $\dot{V}O_2$ response to exercise (for review see Jones et al., 2003). One mechanism that has gained considerable support relates motor unit recruitment patterns to metabolic demands (Burnley et al., 2001, 2002; Sahlin et al., 2005). Burnley et al. (2001) has demonstrated that prior heavy exercise increases the amplitude of the primary rise in $\dot{V}O_2$ during a subsequent bout of heavy exercise. The increase in $\dot{V}O_2$ was later shown by the same authors to be associated with a concomitant increase in integrated sEMG but not mean power frequency (Burnley et al., 2002). These findings are consistent with the view that the increase in the amplitude of $\dot{V}O_2$ is a consequence of additional motor units being recruited in order to generate the required force, but the extent to which less efficient type II motor units are recruited remains an issue of debate (Cleuziou et al., 2004; Scheuermann et al., 2001).

Recently, Sahlin et al. (2005) examined the effect of prior heavy exercise on $\dot{V}O_2$ during a subsequent bout of moderate exercise and found reduction in gross exercise efficiency which the authors related to impaired muscle contractility induced by the prior bout of heavy exercise. However, that study did not assess motor unit recruitment patterns and only speculated that alterations in muscle recruitment may have lead to the lower efficiency. Many previous studies examining the relationship between metabolic requirements and motor unit recruitment patterns have examined the association during heavy intensity exercise that has the added complication that steady-state conditions may not be achieved. Constant work rate exercise in the moderate intensity domain allows for comparisons to be made between established steady-state $\dot{V}O_2$ and motor unit recruitment conditions. Therefore, the purpose of the present study is to examine the effect of prior heavy exercise on the steady-state $\dot{V}O_2$ response and sEMG during a subsequent bout of moderate exercise. While it might be predicted that the O_2 cost of moderate exercise remains independent of prior exercise conditions (i.e. linear dynamic system), we hypothesized that if prior heavy exercise resulted in a higher absolute $\dot{V}O_2$ and $\Delta\dot{V}O_2/\Delta WR$ during a subsequent bout of moderate exercise, the higher O_2 cost would be associated with changes in motor unit recruitment patterns reflecting either an increase in the number of motor units (RMS) and/or the type of motor units recruited (MDPF) as previously suggested (Jones et al., 2003; Sahlin et al., 2005) and reported during repeated bouts of heavy exercise (Burnley et al., 2002).

2. Methods

2.1. Subjects

Eight healthy, male subjects (24.9 ± 2.4 yr) provided written informed consent after being explained all experimental procedures, the exercise protocol, and possible risks associated with participation in the study. The experimental protocol was approved by the Institutional Review Board for Research Involving Human Subjects at Texas Tech University and is in accordance with guidelines set forth by the Declaration of Helsinki.

2.2. Experimental protocol

Subjects reported to the Applied Physiology Laboratory at Texas Tech University on three separate occasions with no less than 48 h between testing sessions. Each subject was instructed to consume only a light meal, and to abstain from vigorous exercise and caffeinated beverages for $\geqslant 12$ h prior to arriving at the Applied Physiology Laboratory for testing. Exercise testing was performed at approximately the same time of the day for each subject. Prior to exercise testing, seat height and handlebar position were adjusted on the cycle ergometer for each subject and returned to the same position for subsequent testing.

Preliminary exercise testing of each subject was performed to both familiarize the subject with testing procedures and for the determination of the estimated lactate threshold (LT) and peak oxygen uptake ($\dot{V}O_{2,peak}$). The highest mean $\dot{V}O_2$ averaged over a 30 s interval was taken as $\dot{V}O_{2,peak}$. All exercise testing was performed on an electrically braked cycle ergometer (Corival 400, Lode, The Netherlands). The initial exercise test involved 4 min of loadless cycling (0 W) followed by progressive exercise to the limit of tolerance in which the work rate increased as a ramp function at a rate of 25 W min^{-1}. For all testing, the subjects were instructed to maintain pedal cadence at 70 rpm that was aided by both visual feedback and verbal encouragement. The estimated LT was determined by visual inspection from gas exchange indices using the V-slope approach, ventilatory equivalents and end-tidal gas tensions. From the results of the ramp test, work rates that would elicit a $\dot{V}O_2$ equivalent to 90% LT (i.e. moderate intensity) and 80% of $\dot{V}O_{2,peak}$ (i.e. heavy intensity) were determined.

On each of the second and third exercise sessions, subjects performed two protocols of constant work rate exercise. Each protocol consisted of alternating step transitions in work rate from a baseline of 20 W to moderate exercise followed by either a second bout of moderate exercise (i.e. moderate–moderate) or by heavy exercise that was followed by a second bout of moderate exercise (i.e. moderate–heavy–moderate). In all protocols, bouts of moderate exercise were 6 min in duration and heavy exercise was performed for 4 min. The second bout of moderate exercise was initiated after 6 min or 30 s of recovery from either moderate or heavy exercise. Different recovery times were used to examine the relationship between $\dot{V}O_2$ and muscle activity during conditions where quite different metabolic requirements would be expected and thus, the coupling between $\dot{V}O_2$ and motor unit recruitment patterns could be purposely challenged. Subjects completed one moderate–moderate protocol (Protocol A, 6 min of recovery between exercise bouts; Protocol B, 30 s of recovery between exercise bouts) followed after at least 15 min of rest by one moderate–heavy–moderate protocol (Protocol C, 6 min of recovery from heavy exercise; Protocol D, 30 s of recovery from heavy exercise) during each visit.

2.3. Measurement of pulmonary gas exchange

Pulmonary gas exchange was measured breath-by-breath using an automated metabolic measurement system (MedGraphics, Model CPX/D, Medical Graphics Corp., St. Pauls, MN). Expired gas flows were measured using a pitot pneumotachograph connected to a pressure transducer. The flow signal was integrated to yield a volume signal that was calibrated with a syringe of known

volume (3.0 l). Prior to each exercise session, the O_2 and CO_2 analyzers were calibrated using gases of known concentrations. Corrections for ambient temperature and water vapor were made for conditions measured near the mouth.

2.4. Measurement of surface electromyography (sEMG)

During each of the protocols, surface electromyography (sEMG) was obtained from the vastus lateralis and vastus medialis muscle groups using a commercially available data acquisition system (PowerLab 8SP, ADInstruments, Grand Junction, CO). The analog sEMG signal was sampled at a rate of 2000 Hz, amplified (common mode rejection ratio: 96 dB, input impedance: 1 MΩ, gain: 5000; Model 408 Dual Bio Amplifier-Stimulator, ADInstruments, Grand Junction, CO), passed through a frequency window of 3-3000 Hz, digitized by a 12-bit A/D converter, and stored on a computer for later analysis. The raw sEMG signal was sampled using bipolar (2×9 mm discs, 15 mm diameter sample area) Ag–AgCL surface electrodes (DDN-30 Norotrode, Myotronics-Noromed, Inc., Tukwila, WA) with a fixed inter-electrode spacing of 30 mm placed on the right leg. The sEMG electrodes were positioned over the distal half of the muscle belly aligned longitudinally to the muscle fibers. A reference electrode was placed over the tibial tuberosity or over the head of the fibula. Electrode sites were shaved and cleaned with alcohol prior to electrode placement in order to reduce inter-electrode resistance (<10 kΩ). All wiring attached to the electrodes was securely fastened to prevent motion artifact. The sEMG signal was checked for motion artifact by moving and tapping the area surrounding the electrode. The site was cleaned again and a new electrode applied if motion artifact was detected in the signal.

2.5. Measurement of plasma lactate

Prior to testing, subjects rested in a supine position while a percutaneous Teflon catheter (22 gauge, Insyte I.V. Catheters, Becton Dickinson, Inc.) was placed into a dorsal hand vein. The blood sample was arterialized by heating the forearm and hand throughout the exercise protocol by use of a heating lamp. Samples were obtained at rest and at 2 min intervals during exercise and recovery in each protocol. Samples were placed in an ice-water slurry and analyzed for plasma lactate concentration ([Lac]) within 5–10 min (Stat Profile M Blood Gas and Electrolyte Analyzer, Nova Biomedical, Inc., Waltham, MA).

2.6. Data analysis

For each subject, $\dot{V}O_2$ was averaged over the last 120 s of the initial baseline cycling (20 W) stage and over the first and last 60 s of each of the steady-state moderate exercise bouts. Since the experimental design required that the recovery duration prior to the second bout of moderate exercise be of variable duration (i.e. 6 min or 30 s), $\Delta\dot{V}O_2/\Delta WR$ was calculated for each subject using the baseline $\dot{V}O_2$ prior to the first bout of moderate exercise for each respective protocol. Net efficiency (ΔEff), defined as the ratio of the change in work accomplished to the change in total energy expenditure, was calculated by utilizing the respiratory exchange ratio and converting the average $\dot{V}O_2$ response to W ($\dot{V}O_2$ (W) = [$\dot{V}O_2$ (ml min^{-1}) 0.001 ml l^{-1} Cal Equiv (kcal l$^{-1}O_2$) 4185 J]/60 s min^{-1}) (Mallory et al., 2002).

Off-line processing of the sEMG signal was performed using a computer program developed in our laboratory using commer-

cially available software (MatLab, The MathWorks Inc., Natick, MA). The raw sEMG signal was passed through a bandpass filter of 20–450 Hz, a notch filter of 60 Hz, and full wave rectified. The root mean square (RMS), a measure of the recruited muscle activity required for force generation, and the median power frequency (MDPF), an indication of the distribution of frequency content, were computed for each muscle. The MDPF was defined by the following equation: $\int_0^{\text{fmed}} S_m(f)\,df = \int_{\text{fmed}}^{\infty} S_m(f)\,df$. $S_m(f)$ is the power density spectrum of the sEMG signal, fmed is the MDPF of the sEMG signal, and f is the frequency in hertz. The RMS and MDPF values during exercise were normalized to baseline cycling at 20 W during the 60 s period prior to the first moderate exercise bout. The normalized RMS and MDPF responses for the vastus lateralis and vastus medialis muscles were averaged together to provide an overall representation of muscle activity during exercise (Burnley et al., 2002). RMS and MDPF were averaged over 5 s intervals, corresponding to the same time interval as for $\dot{V}O_2$ during moderate exercise.

2.7. Statistical analysis

Oxygen uptake ($\dot{V}O_2$), $\Delta\dot{V}O_2/\Delta WR$, RMS, $\Delta RMS/\Delta WR$, $\Delta RMS/\Delta\dot{V}O_2$, MDPF and ΔEff were analyzed using a two-way repeated measures ANOVA design with protocol and time as the main effects. Student–Newman–Keuls post hoc analysis was used to further analyze significant interactions. One-sample t tests were used to test for significant differences from steady-state levels. Statistical significance was accepted when $P < 0.05$. All values are reported as the mean ± SE.

3. Results

3.1. Subjects

On average, subjects weighed 72.1 ± 4.2 kg, were 178.1 ± 2.4 cm tall, and had a body mass index of 20.2 ± 1.2 kg m^2. The group mean aerobic capacity ($\dot{V}O_{2,peak}$) measured during the preliminary ramp exercise test was 45.1 ± 3.2 ml kg^{-1} min^{-1} and the estimated LT was 52.9 ± 2.4% of the $\dot{V}O_{2,peak}$, corresponding to a $\dot{V}O_2$ of 1700 ± 14 ml min^{-1}. The mean work rate for moderate and heavy exercise was 88 ± 10 W and 214 ± 20 W, respectively.

3.2. O_2 Uptake response

The absolute pulmonary $\dot{V}O_2$ response to moderate constant work rate exercise is presented in Table 1. In spite of the considerably different metabolic rates (6 min vs. 30 s recovery) at the onset of exercise, steady-state $\dot{V}O_2$ during the second bout of moderate exercise was similar to that of the first bout in the moderate–moderate transitions (Protocols A and B). In the moderate–heavy–moderate transitions (Protocols C and D), prior heavy exercise resulted in a higher steady-state $\dot{V}O_2$ during the second bout of moderate exercise whether the recovery duration was 6 min or 30 s (1500.2 ± 115.2 ml min^{-1} and 1584.0 ± 124.3 ml min^{-1}, respectively). The elevated absolute $\dot{V}O_2$ was greater for moderate exercise preceded by 30 s of recovery as compared to 6 min of recovery from heavy

Table 1
Comparison of steady-state $\dot{V}O_2$, ΔEff, and sEMG between the first and second bouts of moderate exercise within each protocol

	Protocol A		Protocol B		Protocol C		Protocol D	
	First	Second	First	Second	First	Second	First	Second
$\dot{V}O_2$ (ml min^{-1})	1411 ± 126	1438 ± 135	1413 ± 133	1422 ± 139	1420 ± 132	$1500 \pm 115^{*}$	1418 ± 127	$1584 \pm 124^{*,\#}$
$\Delta\dot{V}O_2$ (ml min^{-1})	588 ± 95	616 ± 102	635 ± 107	645 ± 109	633 ± 112	$714 \pm 89^{*}$	651 ± 115	$818 \pm 103^{*,\#}$
$\Delta\dot{V}O_2/\Delta$WR (ml min^{-1} W^{-1})	9.7 ± 0.4	10.1 ± 0.4	10.3 ± 0.4	10.4 ± 0.7	10.3 ± 0.4	$12.2 \pm 0.7^{*}$	10.7 ± 0.4	$14.1 \pm 0.8^{*,\#}$
ΔEff (%)	29.8 ± 1.3	28.7 ± 1.1	28.0 ± 1.0	28.9 ± 2.9	28.4 ± 1.3	$24.4 \pm 1.5^{*}$	27.2 ± 1.1	$21.0 \pm 1.4^{*}$
RMS (μV · s^{-1})	0.11 ± 0.02	0.11 ± 0.02	0.10 ± 0.02	0.11 ± 0.01	0.10 ± 0.01	0.11 ± 0.01	0.11 ± 0.02	0.11 ± 0.01
ΔRMS/ΔWR (%W)	1.7 ± 1.9	1.8 ± 0.3	2.0 ± 0.3	2.0 ± 0.4	1.8 ± 0.2	2.1 ± 0.3	2.0 ± 0.2	2.2 ± 0.3
ΔRMS/$\Delta\dot{V}O_2$ (μV · l^{-1} min^{-1})	0.09 ± 0.01	0.09 ± 0.02	0.09 ± 0.01	0.10 ± 0.02	0.09 ± 0.02	0.09 ± 0.02	0.10 ± 0.02	0.08 ± 0.02
MdPF (Hz)	69.1 ± 2.9	$71.2 \pm 3.3^{*}$	68.2 ± 1.8	$70.0 \pm 2.0^{*}$	70.3 ± 2.5	$71.9 \pm 2.3^{*}$	72.2 ± 3.5	72.0 ± 3.3

Values are mean ± SE.

  [*] Significant difference ($P < 0.05$) between bouts of moderate exercise within the same protocol.

  [#] Significant difference ($P < 0.05$) between the second bout of moderate exercise in Protocols C and D.

exercise ($P < 0.05$). Interestingly, the higher absolute $\dot{V}O_2$ during the second bout of moderate exercise in the moderate–heavy–moderate transitions was negatively correlated with aerobic capacity (i.e. fitness level) such that individuals with the lower $\dot{V}O_{2,peak}$ exhibited the largest increase in $\dot{V}O_2$ following heavy exercise ($r = 0.54$, $F = 5.87$, $P < 0.05$).

3.3. Vastus muscle sEMG activity

The average RMS and MdPF response from the vastus lateralis and vastus medialis muscles during moderate constant work rate cycling exercise are presented in Table 1. No difference in RMS or the percent change in RMS from 20 W cycling was observed between bouts of moderate exercise within any of the four constant work rate exercise protocols despite changes in the O_2 cost of exercise (Fig. 1). In contrast, MdPF was increased by 2–3% during the second bout of moderate exercise in the moderate–moderate transitions (Protocols A and B), and also during the moderate–heavy–moderate transition with the 6 min recovery (Protocol C). However, MdPF remained unchanged between the first and second bouts of moderate exercise when the second bout of moderate exercise was preceded by 30 s of recovery from heavy exercise (Protocol D; see Table 1). Interestingly, MdPF expressed as the percent change from 20 W cycling was found to be $46.8 \pm 8.7\%$ lower than the average response during the first minute of the second bout of moderate exercise when preceded by 30 s of recovery from heavy exercise (Protocol D, Fig. 1). The change in MdPF was not correlated with the increase in $\dot{V}O_2$ ($r = 0.17$, $F = 0.80$, $P = 0.38$).

The ratio of RMS to cycling work rate (ΔRMS/ΔWR) showed a constant level during all moderate exercise bouts indicating a coupling between motor unit recruitment and cycling work rate (Table 1). The relationship between RMS and $\dot{V}O_2$ was examined by the ΔRMS/$\Delta\dot{V}O_2$ ratio which was increased during the first minute of moderate exercise when preceded by 6 min of recovery from either moderate or heavy exercise, but reduced when preceded by 30 s of recovery when $\dot{V}O_2$ (i.e. metabolic rate) was ele-
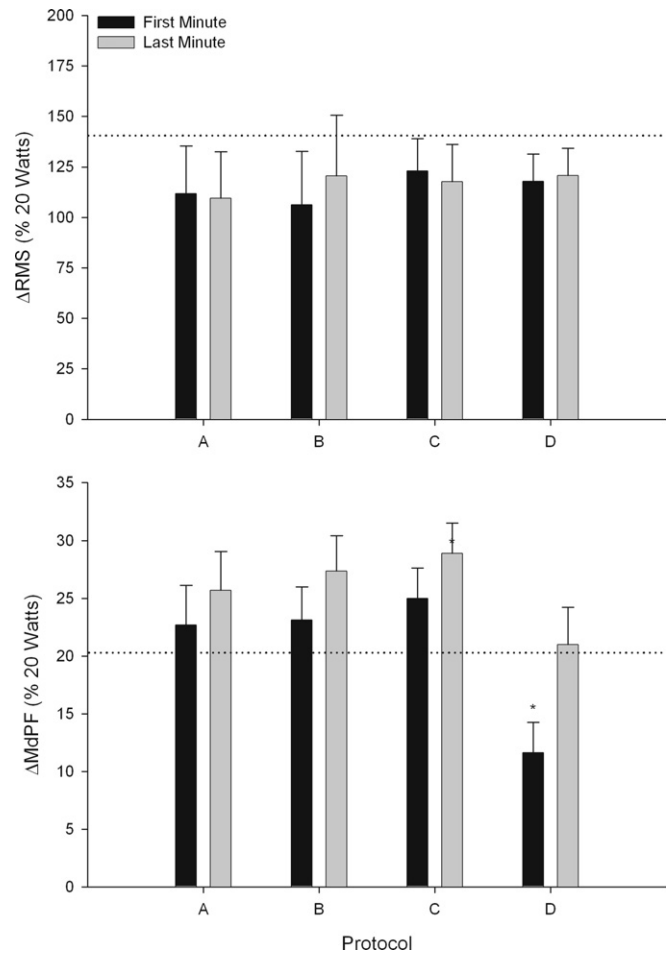

Fig. 1. Changes in vastus muscle activity during the first and last minute of the second bout of moderate exercise. Upper panel: The increase in RMS from 20 W cycling (ΔRMS) reached a stable level of motor unit recruitment at exercise onset that did not vary or change with prior heavy exercise. Lower panel: The increase in MdPF from 20 W cycling (ΔMdPF) was similar between the first and last minute of moderate exercise during the moderate–moderate transitions, but varied from the average response during the moderate–heavy–moderate transitions. Dotted lines represent the average steady-state value reached during the first bout of moderate exercise in the four protocols combined. (*) Significant difference between first and last minute of moderate exercise within each protocol ($P < 0.05$).
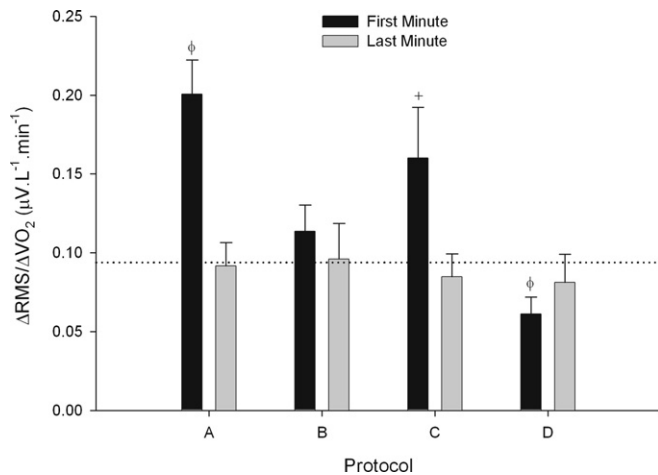
Fig. 2. The ratio of RMS to $\dot{V}O_2$ ($\Delta RMS/\Delta \dot{V}O_2$) was increased at the onset of exercise when 6 min of recovery was present before the second bout of moderate exercise. $\Delta RMS/\Delta \dot{V}O_2$ showed a reduction under conditions of high metabolic rate at exercise onset. During the last minute of exercise, $\Delta RMS/\Delta \dot{V}O_2$ was similar to the average steady-state value calculated during the first bout of moderate exercise shown as the dotted line. (*) Significant difference between first and last minute of moderate exercise within each protocol ($P < 0.05$).

vated (Fig. 2). During the last minute of the second bout of moderate exercise, $\Delta RMS/\Delta \dot{V}O_2$ ratio returned to the average steady-state ratio measured during the first bout of moderate exercise in all the exercise protocols irrespective of the prior exercise conditions.

3.4. Gain and exercise efficiency

The gain or $\Delta \dot{V}O_2/\Delta WR$ for moderate exercise paralleled the $\dot{V}O_2$ response and is presented in Table 1. Moderate–moderate exercise transitions (Protocol A and B) did not lead to a difference in $\Delta \dot{V}O_2/\Delta WR$ which remained at ~10 ml min^{-1} W^{-1} in spite of the different recovery metabolic rates prior to the onset of the second bout of moderate exercise. In contrast, prior heavy exercise increased $\Delta \dot{V}O_2/\Delta WR$ to 12.2 ± 0.7 ml min^{-1} W^{-1} and 14.1 ± 0.8 ml min^{-1} W^{-1} during the second bout of moderate exercise as compared to the first bout of moderate exercise when preceded by 6 min and 30 s of recovery from heavy exercise, respectively ($P < 0.05$). The increase in $\Delta \dot{V}O_2/\Delta WR$ during the second bout of moderate exercise was greater after 30 s of recovery (i.e. high metabolic rate) as compared to 6 min of recovery from heavy exercise (Protocol D > Protocol C, $P < 0.05$; Fig. 3).

Net efficiency or ΔEff calculated during steady-state moderate exercise is presented in Table 1. During the moderate–moderate exercise transitions, ΔEff was not different between the first and second bout of moderate exercise. However, prior heavy exercise resulted in a decrease in ΔEff by $-13.3 \pm 5.6\%$ and $-22.2 \pm 4.9\%$ during the second bout of moderate exercise as compared to the average steady-state response for Protocols C and D, respectively (Fig. 3, $P < 0.05$).
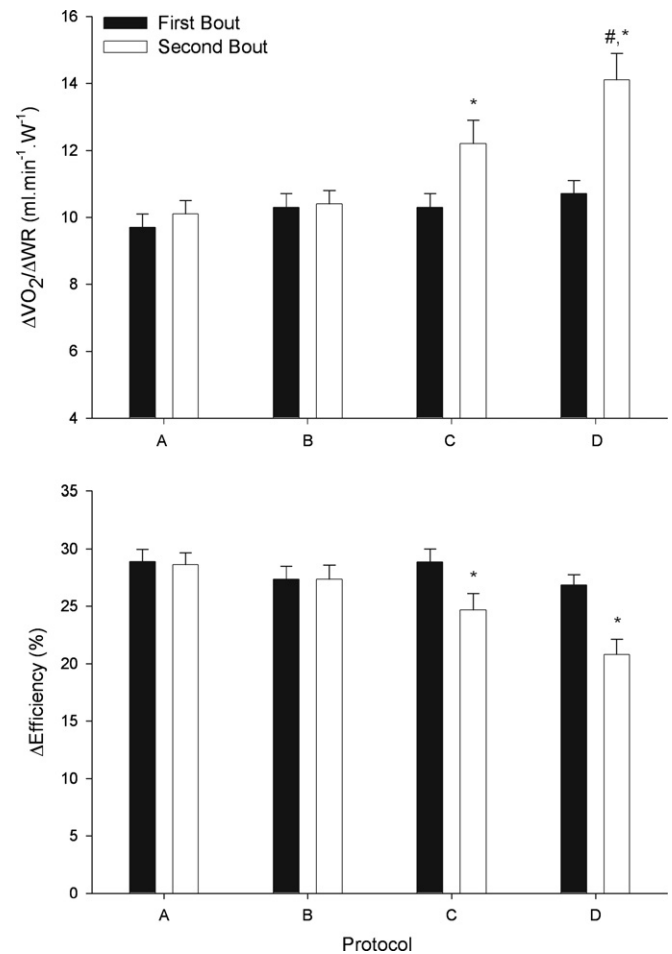

Fig. 3. Changes in gain ($\Delta \dot{V}O_2/\Delta WR$) and net efficiency ($\Delta Eff$) during the last minute of moderate exercise for each protocol. Prior heavy exercise resulted in a higher gain and a decrease in exercise efficiency during the second bout of moderate exercise. (*) Significant difference between first and second bout of moderate exercise within each protocol ($P < 0.05$). (#) Significant difference between the second bouts of moderate exercise in Protocols C and D ($P < 0.05$).

3.5. Plasma lactate

The plasma [Lac] response following heavy exercise was analyzed for differences in the rate of [Lac] clearance into the blood during the second bout of moderate exercise in the moderate–heavy–moderate transitions (Protocols C and D, Fig. 4). On average, plasma [Lac] increased from 1.6 mmol · l^{-1} at rest to a peak level of 9.3 ± 1.0 mmol · l^{-1} and 9.6 ± 1.0 mmol · l^{-1} 3 min after heavy exercise for Protocols C and D, respectively. Although the second bout of moderate exercise was initiated either 6 min or 30 s after heavy exercise, the recovery profile of plasma [Lac] was similar between Protocols C and D when time was aligned to the end of heavy exercise rather than to the onset of the moderate intensity exercise. Correlation analyses did not reveal a relationship between plasma [Lac] and $\dot{V}O_2$ ($r = 0.009$, $F = 0.003$, $P = 0.96$), MdPF ($r = -0.27$, $F = 2.26$, $P = 0.14$), $\Delta \dot{V}O_2/\Delta WR$ ($r = 0.20$, $F = 1.15$, $P = 0.29$), or ΔEff ($r = 0.14$, $F = 0.59$, $P = 0.45$) during the second bout of moderate exercise in Protocols C and D.
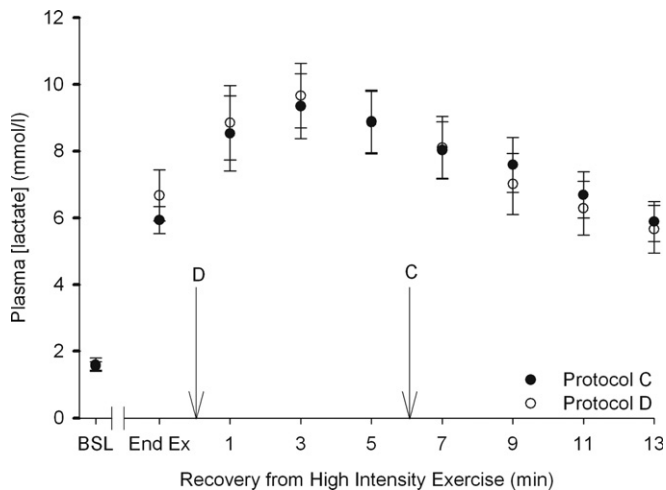
Fig. 4. Plasma lactate [Lac] measurement following heavy exercise in Protocols C and D. Arrows denote the beginning of moderate exercise for Protocols C and D. There was no difference in the recovery of plasma [Lac] between the two moderate–heavy–moderate transitions.

4. Discussion

Prior heavy exercise has consistently been shown to increase both absolute $\dot{V}O_2$ and the O_2 cost (as both $\Delta\dot{V}O_2/\Delta WR$ and ΔEff) during a subsequent bout of exercise for both moderate (Sahlin et al., 2005) and heavy constant work rate exercise (Burnley et al., 2001, 2002; Scheuermann et al., 2001). The contribution of motor unit recruitment to the elevated $\dot{V}O_2$ remains uncertain and has received relatively little attention during the steady-state of moderate intensity exercise. Consistent with the recent study by Sahlin et al. (2005), the present study found prior heavy exercise to decrease exercise efficiency during a subsequent bout of moderate exercise. We further showed heavy exercise to increase the gain during a subsequent bout of moderate exercise. However, in contrast to our hypothesis, the increased O_2 cost during moderate exercise was not associated with either the recruitment of additional motor units, since RMS remained unchanged, or the recruitment of less efficient type II motor units, since the change in MDPF was not related to changes in $\dot{V}O_2$. These findings suggest that the mechanism(s) causing the increased O_2 cost during prior heavy exercise conditions is not solely related to alterations in motor unit recruitment patterns as assessed by sEMG.

4.1. sEMG and moderate constant work rate exercise

The observation of a rapid increase of RMS to a constant level during moderate constant work rate exercise is not a new finding and has been demonstrated to occur in both untrained and trained subjects during cycling exercise (Jammes et al., 1998). Petrofsky (1979) has further shown RMS of the quadriceps to remain unchanged during prolonged (80 min) moderate exercise at cycling intensities of 20–40% $\dot{V}O_{2\,max}$ and for at least 20 min during moderate exercise at 60% $\dot{V}O_{2\,max}$. It is at high intensities (>60% $\dot{V}O_{2max}$) that RMS has been shown to increase with time during moderate

constant work rate exercise (Petrofsky, 1979), a response that is likely influenced by the trained-state of muscle (Hug et al., 2004). The present study is consistent with these findings by showing an invariable RMS during 6 min of moderate exercise at 90% LT despite prior moderate or heavy exercise and an elevated metabolic rate at the onset of exercise. This finding provides good evidence that the amplitude of motor unit recruitment is not associated with the elevated O_2 cost during the second bout of moderate exercise, but rather is closely coupled to work rate and presumably force requirements since pedal cadence and therefore pedal torque remained relatively constant during the exercise.

Although RMS reflects overall motor unit recruitment, RMS does not provide information regarding the type of motor units contributing to the measured myoelectrical signal. It is possible that the composition of muscle fiber types that make up the RMS signal may change following heavy exercise as type I fibers are progressively replaced by type II fibers in the presence of muscle fatigue. Median power frequency has often been used to provide information about the type of motor units recruited with type I fibers having a lower firing frequency than type II fibers in the power density spectrum of the sEMG signal (Kupa et al., 1995). Several studies have shown that the frequency content (mean or median) remains unchanged during incremental cycling exercise to exhaustion (Gamet et al., 1993; Jansen et al., 1997; Petrofsky, 1979; Scheuermann et al., 2002; Viitasalo et al., 1985) which is quite different from the shift in spectral information that occurs during localized fatiguing muscle contractions as additional type II motor units are recruited in an attempt to maintain force requirements (De Luca, 1984). Given that most of the exercise in the present study was performed in the moderate domain and that heavy exercise was only brief, the need to recruit additional motor units or to recruit type II motor units due to fatigue would not be large. The small increase ($\sim$3%) in absolute MDPF found in the present study during the second bout of moderate exercise in both moderate–moderate and moderate–heavy–moderate (Protocol C only) transitions is not likely a result of muscle fatigue, but a pattern of muscle activity that has been reported to occur during moderate and severe constant work rate exercise (Cleuziou et al., 2004). During cycling exercise at 80% LT, Cleuziou et al. (2004) has reported MDPF to progressively increase in the vastus lateralis and vastus medialis after 2–3 min of exercise onset reaching a 2–4% increase after 6 min of exercise. Like the present study, Cleuziou et al. (2004) did not find the increase in MDPF to be associated with $\dot{V}O_2$, but suggested that the augmented MDPF may be the result of increased motor neuron discharge rate of type I muscle fibers, a turnover in type I motor units, or a rise in muscle temperature which could increase conduction velocity (Bigland-Ritchie et al., 1981).

When expressed as a percent of 20 W cycling, MDPF was found to increase by 6% during the second bout of moderate exercise following 6 min of recovery from heavy exercise (Protocol C). Although tempting to relate the increase in MDPF to the 7% increase in $\dot{V}O_2$, 20% increase

in $\Delta\dot{V}O_2/\Delta WR$, or 13% decrease in ΔEff measured during this same bout, it should be restated here that no correlation was found between MDPF and any of these variables in absolute or relative comparisons. Furthermore, if MDPF was responsible for the increased O_2 cost during the second bout of moderate exercise it should follow that MDPF would be increased in both moderate–heavy–moderate exercise transitions since $\Delta\dot{V}O_2/\Delta WR$ and ΔEff were both found to be significantly altered in both Protocols C and D. This was not the case as shown by the average rise in MDPF to steady-state level during the second bout of moderate exercise in Protocol D (Fig. 1). Therefore, it is reasonable to conclude that MDPF was not associated with the increased O_2 cost during moderate exercise.

4.2. Variation in $\Delta RMS/\Delta\dot{V}O_2$ ratio during moderate exercise

Recently, the relationship between $\dot{V}O_2$ and motor unit recruitment, as assessed by RMS, has been investigated through the examination of the $\Delta RMS/\Delta\dot{V}O_2$ ratio. During moderate constant work rate exercise, Jammes et al. (1998) has shown $\Delta RMS/\Delta\dot{V}O_2$ ratio to increase at the onset of exercise due to the slower adjustment of $\dot{V}O_2$ as compared to RMS to a step increase in work rate. Following 2 min of exercise, $\Delta RMS/\Delta\dot{V}O_2$ ratio decreased to a constant ratio once $\dot{V}O_2$ reached a steady-state suggesting a coupling between motor unit recruitment and $\dot{V}O_2$. In agreement with previous reports (Arnaud et al., 1997; Hug et al., 2004; Jammes et al., 1998), the present study found $\Delta RMS/\Delta\dot{V}O_2$ ratio to be highest during the first minute of moderate exercise, but lowered to a steady-state level when examined during the last minute of moderate exercise. However, a novel finding of the present study is that the adjustment of $\Delta RMS/\Delta\dot{V}O_2$ ratio is influenced by prior metabolic rate such that under conditions of high metabolic rate (30 s recovery, Protocol B and D) the normal increase in $\Delta RMS/\Delta\dot{V}O_2$ ratio at the onset of the second bout of moderate exercise is reduced, significantly more so following prior heavy exercise. Under this condition, the $\dot{V}O_2$ response to moderate exercise is in excess of the average metabolic requirement and may be partly utilizing anaerobic pathways following heavy exercise as suggested by the elevated plasma [Lac] (first minute = 8.8 ± 1.2 mmol $\cdot l^{-1}$) measured in the present study. In this environment of an augmented O_2 cost and raised plasma [Lac] during moderate exercise, the recruitment of motor units remains coupled to work rate and is not observed to vary. This observation is in contrast to the concept of RMS adjusting to $\dot{V}O_2$ as described by others to possibly occur under anaerobic conditions to decrease the muscles requirement for energy (Arnaud et al., 1997; Hug et al., 2004; Jammes et al., 1998).

4.3. Different baseline metabolic rates at exercise onset

Recovery duration was either 6 min or 30 s in an attempt to examine the effect of baseline metabolic rate

(i.e. $\dot{V}O_2$) on the second bout of moderate exercise. This approach was utilized to emphasize any difference between the O_2 cost of exercise from the motor unit recruitment response by initiating exercise during conditions where $\dot{V}O_2$ had nearly recovered to baseline values and when $\dot{V}O_2$ remained appreciably elevated during recovery from prior exercise. It was found that RMS was not influenced by baseline metabolic rate since the percent increase in RMS from 20 W was similar during the first minute of moderate exercise for all exercise protocols. In contrast, at the onset of moderate exercise under conditions of high baseline metabolic rate following heavy exercise, MDPF was found to be 47% lower than the average steady-state value during the first minute of moderate exercise. The decreased MDPF was a result of prior heavy exercise since the same change in MDPF was not observed during the moderate–moderate exercise transition with the same recovery duration (30 s). The reduced MDPF is also not the result of increased plasma [Lac] since no correlation was found between the two variables ($r = 0.27$). These findings are consistent with the study by Jansen et al. (1997) during incremental cycling exercise where MDPF of the vastus lateralis was found to significantly decrease within the first minute of recovery, a change that was not reported to be correlated with plasma [Lac]. The mean decrease was 9 Hz which is similar to the 8 Hz fall measured in the present study. The mechanism causing the decrease in MDPF following heavy exercise is unclear, but it is possible that it is related to changes in extracellular potassium (K^+). Action potential transduction is reliant upon effective Na^+/K^+ gradients. Therefore an increase in K^+, as would occur during repeated muscle contractions, would impair conduction velocity and reduce motor unit firing frequency. Poole et al. (1991) has reported an increase in serum [K^+] during severe cycling exercise. If a similar rise occurs during heavy exercise, it is plausible that [K^+] would still be elevated after a 30 s recovery from heavy exercise and would cause a decrease in MDPF. This is only speculation since [K^+] was not measured in the present study.

4.4. Selection of vastus muscles examined during cycling exercise

The present study did not find an association between sEMG, analyzed in the time domain (RMS) and frequency domain (MDPF), and changes in $\dot{V}O_2$ or O_2 cost during moderate cycling exercise that was performed after a bout of heavy exercise. Our examination of sEMG comes from two leg muscles, the vastus lateralis and vastus medialis, which are the primary muscles recruited during cycling exercise (Ericson et al., 1985) and therefore, may provide a reasonable description of motor unit recruitment pattern. Support for this has been provided by Poole et al. (1992) using the direct Fick method. These authors found the $\dot{V}O_2$ across the exercising limb to account for approximately 75–84% of the whole body $\dot{V}O_2$ during moderate cycling exercise, indicating that the muscles of the thigh are the most

metabolically active muscles during moderate intensity cycling. Furthermore, it was demonstrated that blood flow was only 4–8% higher in the inferior vena cava compared to that measured in the femoral vein suggesting that the contribution of any venous drainage not accounted for at the femoral vein (e.g. drainage from the gluteal muscles) was insignificant. Thus, we believe that the sEMG of the vastus lateralis and vastus medialis provides a good representation of muscle activity occurring during cycling exercise.

5. Conclusion

A reduction in exercise efficiency (i.e. O_2 cost) can be detrimental to exercise performance for sports involving muscular work that lasts longer than 30 s. Therefore, the identification of factors that alter the O_2 cost of exercise is important not only for the athlete, but also for the individual burdened by disorders of the cardiopulmonary and metabolic systems. The present study shows that the elevated O_2 cost of exercise reported by others to occur following heavy intensity exercise is not a result of a greater recruitment of motor units or an appreciable recruitment of less efficient type II muscle fibers during moderate exercise. These results indicate that heavy exercise promotes an additional demand for O_2 that is in excess to that normally defined by moderate exercise causing a decrease in the efficiency of muscular work. To the athlete and patient this reflects an additional stress on the cardiovascular system during moderate exercise that may alter functional capacity or prolong recovery. Interestingly, an inverse relationship was identified for aerobic capacity (i.e. fitness level) and the change in exercise efficiency following heavy exercise. Clearly, further examination into the mechanism causing the elevated O_2 cost is warranted.

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