J Musculoskelet Neuronal Interact 2019; 19(3):266-275

Journal of Musculoskeletal and Neuronal Interactions JMNI

Original Article

Time course of changes in neuromuscular responses during rides to exhaustion above and below critical power

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Abstract

Objectives: To examine the time course of changes in electromyographic (EMG) and mechanomyographic (MMG) amplitude (AMP) and mean power frequency (MPF) responses during cycle ergometry to exhaustion performed above ($CP_{+10\%}$) and below ($CP_{-10\%}$) critical power (CP) to infer motor unit activation strategies used to maintain power output. **Methods:** Participants performed a 3-min all out test to determine CP, and 2 randomly ordered, continuous rides to exhaustion at $CP_{+10\%}$ and $CP_{-10\%}$. $\dot{V}O_2$, EMG AMP, EMG MPF, MMG AMP, MMG MPF, and time to exhaustion (T_{lim}) were recorded. Responses at $CP_{-10\%}$ and $CP_{+10\%}$ were analyzed separately. **Results:** At $CP_{-10\%}$, EMG and MMG AMP were significantly greater than the initial 5% timepoint at 100% T_{lim}. EMG MPF and MMG MPF reflected a downward trend that resulted in no significant difference between timepoints. At $CP_{+10\%}$, EMG AMP was significantly greater than the initial 5% timepoint from 60% to 100% T_{lim}. MMG AMP was less than the initial 5% timepoint at only 50% T_{lim}. EMG and MMG MPF were significantly less than the initial 5% timepoint at 20% T_{lim} and 100% T_{lim}, respectively. **Conclusions:** The time-course of changes in EMG and MMG signals were different at $CP_{-10\%}$ and $CP_{+10\%}$, but responses observed indicated cycle ergometry to exhaustion relies on similar motor unit activation strategies.

Keywords: Electromyography, Mechanomyography, Onion Skin Scheme, Muscular Wisdom, Cycle Ergometry

Introduction

Critical power (CP) is the asymptote of the power duration curve and, theoretically, reflects the highest power output that can be maintained without fatigue[1,2]. Cycle ergometry performed at or below (CP minus 10 to 15 percent) CP can typically be maintained for 20-60 minutes with little to no evidence of metabolic or neuromuscular fatigue[3-6]. There are a number of applications of the CP model including the assessment of fitness levels[7], examination of the efficacy of training programs[7], and the demarcation of the heavy and severe exercise intensity domains[4]. Previous studies have used CP as the demarcation of the heavy and severe domains to examine neuromuscular responses during continuous cycle ergometry to further understand the motor unit activation strategies under various levels of fatigue[3,8,9].

The electromyographic (EMG) and mechanomygraphic (MMG) signals have been used to examine neuromuscular responses during exhaustive work bouts[3,8-10]. The information contained within the EMG and MMG signals can be used to make inferences regarding the motor unit activation strategies used during fatiguing and non-fatiguing tasks[11-13]. Electromyography represents the electrical component of muscular work[14], while MMG detects the mechanical component of the generation of lateral oscillations from the "...slow bulk lateral movement of the muscle related to the different regional distribution of the contractile elements"[15], additional oscillations occurring at the resonant frequency of the muscle[15-17], and pressure waves produced by the dimensional changes of active muscle fibers[15,18]. The EMG and MMG signals contain both an amplitude (AMP) and frequency (mean power frequency: MPF) domain. It has been suggested the fatigue-induced increases in EMG AMP during exhaustive, dynamic exercise reflect the

The authors have no conflict of interest.

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Edited by: G. Lyritis
Accepted 19 March 2019

recruitment of additional motor units, changes in the motor unit firing rates, and/or synchronization, while decreases in EMG MPF reflect the slowing of the motor unit action potential conduction velocity (MUAP CV)[14,19]. Furthermore, under some conditions, MMG AMP reflects motor unit recruitment, and the MPF reflects the global motor unit-firing rate of activated, unfused muscle fibers[20]. During fatiguing tasks, increases in MMG AMP suggest greater motor unit recruitment, while decreases in MMG MPF reflect a decrease in the firing rate[20,21]. Therefore, the simultaneous assessment of the EMG and MMG signals during a fatiguing task can provide insight into the motor unit activation (changes in motor unit recruitment and firing rate) strategies used to maintain force production or power output[22].

Previous studies[8-10] have used EMG and MMG responses during cycle ergometry performed at CP and various power outputs to examine the neuromuscular patterns of responses during fatiguing tasks. No change or increases over time have been reported for EMG AMP (muscle activation), depending on the power output the ride was performed (50-95% peak power), the muscle measured (vastus lateralis vs. vastus medialis), and the mathematical model used to derive CP (3-min all out vs. 3-parameter nonlinear)[3,8,10]. For MMG AMP, the responses were dependent on the power output the ride was performed at and the mathematical model used to estimate CP. Specifically, at lower intensities (50-65% peak power) and rides performed at CP estimated from the 3-parameter nonlinear model (56 ± 5% peak power), MMG AMP decreased over time, while exercise at higher intensities (80-95% peak power) and CP estimated from the 3-min all out test (81 ± 6% peak power) resulted in no change or increases in MMG AMP over time[3,9,10]. Furthermore, rides performed at CP estimated from the 3-min all out test have resulted in increases in EMG MPF (CP= 78 ± 7% peak power), but no change in MMG MPF (CP= 81 ± 6% peak power)[8,9]. These findings suggest the patterns of neuromuscular responses differ between the muscles measured and are dependent upon the power output and duration of the fatiguing task, but little is known about the time course of changes in these responses during cycle ergometry.

Recently, investigators have combined polynomial regression analyses and analysis of variance (ANOVA) with post-hoc Student Newman-Keuls to examine the time course of changes in neuromuscular parameters during fatiguing, sustained isometric, intermittent isometric, and dynamic constant external resistance muscle actions of the leg extensors[22-24]. The application of this unique analysis allows for the identification of the time course of changes in neuromuscular responses during a fatiguing task[22,25]. Identification of the time course of changes in neuromuscular parameters can be used to make inferences regarding fatigue related changes in motor unit activation strategies (Onion Skin Scheme, Muscular Wisdom, and the after-hyperpolarization theory)[11-13]. Specifically, the Onion Skin Scheme hypothesizes force production during fatiguing tasks is maintained by increasing muscle activation (EMG AMP) and recruitment of higher threshold motor units (MMG AMP) that have lower firing rates (MMG MPF) than previously activated motor units[11,26]. The Onion Skin Scheme suggests there are competing influences on the global motor unit firing rate from increases in the firing rates of already recruited motor units, and the newly recruited motor units (higher threshold fibers) which have lower firing rates than those previously recruited. Muscular Wisdom is also characterized by increases in EMG and MMG AMP (muscle activation and motor unit recruitment, respectively) and decreases in MMG MPF (motor unit firing rate)[13]. Muscular Wisdom, however, explains the decrease in MMG MPF as a decrease in relaxation time of the whole muscle and in motor unit firing rate, providing greater twitch fusion and an economical activation of previously recruited motor units[13,27]. The after-hyperpolarization strategy is characterized by increases in EMG AMP, EMG MPF, and MMG MPF resulting from greater after-hyperpolarization due to increased fatigue-induced metabolites shifting potassium from intracellular to extracellular[12]. This then leads to the central nervous system increasing motor unit recruitment and motor unit firing rate to maintain force production[12]. No previous studies, however, have examined the time course of changes in neuromuscular responses during cycle ergometry to exhaustion. Therefore, the purpose of the present study was to examine the time course of changes in neuromuscular (EMG AMP, EMG MPF, MMG AMP, and MMG MPF) responses during rides to exhaustion performed above and below CP, and to make inferences regarding the motor unit activation strategies used to maintain power output.

Materials and methods

Experimental design

This study consisted of four visits, separated by a minimum of 24 to 48 hours. During the first visit, the peak oxygen consumption rate ($\dot{V}O_{2peak}$) and gas exchange threshold (GET) were determined from a graded cycle ergometer test to exhaustion (GXT). Critical power was determined from the 3-min all-out test during the second visit. The third and fourth visits consisted of two randomly ordered, continuous rides to exhaustion at CP minus 10% ($CP_{-10\%}$) and CP plus 10% ($CP_{+10\%}$). Metabolic and neuromuscular responses as well as times to exhaustion (T_{lim}) were recorded during each of the continuous rides.

Participants

Eleven recreationally trained participants (six females and five males, mean ± SD age: 21 ± 2 year; body weight 70 ± 14 kg; height 171 ± 10 cm) volunteered for this study. The participants took part in one, or a combination, of the following physical activities; running (n=8), cycling (n=6), and recreational sports (n=3). These data are part of a larger data set with multiple independent and dependent variables, which have been previously published[28,29]. This study was approved by the University Institutional Review Board for Human Subjects and all participants completed a health history questionnaire and signed a written informed consent document before testing.

Determination of peak oxygen consumption rate and the gas exchange threshold

Each participant performed a GXT on a calibrated Lode (Corval V3, Groningen, the Netherlands) electronically-braked cycle ergometer at a pedal cadence of 70 rev·min^{-1}. The ergometer seat height was adjusted so that the participant's legs were near full extension at the bottom of the pedal revolution. Toe clips were used to maintain pedal contact throughout the test. Each participant wore a nose clip and breathed through a 2-way valve (Hans Rudolph 2700 breathing valve, Kansas City, MO, USA). Expired gas samples were collected and analyzed using a calibrated TrueMax 2400 metabolic cart (Parvo Medics, Sandy, UT, USA). The gas analyzers were calibrated with room air and gases of known concentration prior to all testing sessions. O_2, CO_2, and ventilatory parameters were recorded breath-by-breath and expressed as 10 s averages. Heart rate was recorded with a Polar Heart Watch system (Polar Electro Inc., Lake Success, NY). The test began at 50 W and the power output was increased by 30 W every 2 min until voluntary exhaustion or the participant's pedal rate fell below 70 rev·min^{-1} for more than 10 s, despite strong verbal encouragement. The peak oxygen consumption rate ($\dot{V}O_{2peak}$) was defined as the highest $\dot{V}O_2$ value in the last 60 s of the test. The power output associated with $\dot{V}O_{2peak}$ (W) was defined as the power output at $\dot{V}O_{2peak}$ (p$\dot{V}O_{2peak}$). The GET was determined using the V-slope method as described by Beaver, Wasserman, and Whipp[30]. The GET was defined as the $\dot{V}O_2$ value corresponding to the intersection of two separate regression lines in the breakpoint of the $\dot{V}CO_2$ versus $\dot{V}O_2$ relationship. The GET was used to determine the resistance setting for the CP 3-min all-out test.

Critical power test

Critical power was determined from the 3-min all-out test, on the electronically-braked cycle ergometer, using the procedures adapted from Burnley, Doust, and Vanhatalo[31] and Vanhatalo, Doust, and Burnley[32]. Prior to the test, each participant completed a warm-up at 50 W for 5 min followed by 5 min of rest. The resistance for the test was set using the linear mode of the electronically-braked cycle ergometer (linear factor= power/cadence^2). The linear factor was calculated as the power output halfway between $\dot{V}O_{2peak}$ and GET (GET + 50% Δ) divided by a cadence of 70 rev·min^{-1} squared[32]. Thus, the linear factor was equal to GET + 50% Δ/(70 rev·min^{-1})^2. The test began with unloaded cycling at 70 rev·min^{-1} for 3 min. During the last 5 s of the unloaded phase, the participant was instructed to increase the pedaling cadence to 110 rev·min^{-1} and then maintain the cadence as high as possible throughout the 3 min all-out effort at the determined resistance. To prevent pacing and ensure an all-out effort, the participant was not informed of the elapsed time and strong verbal encouragement was provided. Critical power was the average power output over the final 30 s of the test.

Continuous rides to exhaustion at $CP_{-10\%}$ and $CP_{+10\%}$

Two, randomly ordered, continuous rides at $CP_{-10\%}$ and $CP_{+10\%}$ were completed on separate days. Prior to testing, each participant completed a 5-minute warm-up at 50 W on the electronically-braked cycle ergometer. After a five-min rest, the power output was set at $CP_{-10\%}$ or $CP_{+10\%}$ and the power output was maintained at 70 rev·min^{-1}. The test was terminated when the participant's pedal rate fell below 70 rev·min^{-1} for more than 10 seconds, despite strong verbal encouragement or at 60 min. The T_{lim} for $CP_{-10\%}$ and $CP_{+10\%}$ was recorded.

Electromyography and mechanomyography measurements

During the GXT as well as the rides at $CP_{-10\%}$, and $CP_{+10\%}$, a bipolar surface EMG electrode (circular 4 mm diameter, silver/silver chloride, Biopac Systems, Inc., Santa Barbara, CA) arrangement (30 mm inter-electrode distance) was placed on the vastus lateralis muscle of the right thigh. Prior to electrode placement, the skin at each site was shaved, carefully abraded, and cleaned with alcohol. The EMG electrodes were placed based on the recommendations from the SENIAM Project for EMG electrodes placement[33]. Specifically, a reference line was drawn over the vastus lateralis one-third of the distance between the lateral superior border of the patella and the anterior superior iliac crest. In addition, the electrode placement site was located 5 cm lateral to the reference line so that the electrodes would lie over the vastus lateralis muscle[34]. A goniometer (Smith & Nephew Rolyan, Inc., Menomonee Falls, WI) was used to orient the EMG electrodes at a 20° angle to the reference line to approximate the pennation angle of the muscle fibers for the vastus lateralis[35]. The reference electrode was placed over the iliac crest. The EMG signals were differentially amplified (EMG 100c, BIOPAC Systems, Inc., Santa Barbara, CA, USA, bandwidth= 10-500 Hz, gain: ×1,000), and digitally bandpass filtered (zero-phase shift fourth-order Butterworth) at 10-500 Hz.

The MMG signals were detected with an accelerometer (Entran EGAS FT 10, bandwidth 0-200 Hz, dimensions: 1.0 x 1.0 x 0.5 cm, mass 1.0 g sensitivity 10 mV g^{-1}) placed on the vastus lateralis muscle between the bipolar electrode arrangement using double-sided adhesive tape. The accelerometer used in the present study was consistent with the accelerometer used in previous studies[36,37] that have examined MMG responses during cycle ergometry. The signal was analyzed from the sensitive axis of the accelerometer positioned perpendicular to the skin surface. The other sensitive axis was positioned along the longitudinal axis of the muscle.

Signal processing

The raw EMG and MMG signals were sampled at 1 kHz with a 16-bit analog-to-digital converter (Model MP150, BIOPAC

Systems, Inc., Santa Barbara, CA, USA). The signals were recorded and stored in a personal computer and the amplitude (microvolts root mean square, μVrms) values were calculated off-line using a custom program written with LabVIEW programming software (version 8.5, National Instruments, Austin, TX). The EMG and MMG signals were zero-meaned and bandpass filtered (fourth-order Butterworth) at 10-500 Hz and 5-100 Hz, respectively. The EMG and MMG amplitude (root mean square; AMP) and frequency (mean power frequency; MPF) values were calculated for 10 second epochs throughout the GXT as well as the $CP_{-10\%}$ and $CP_{+10\%}$ rides. The EMG AMP, EMG MPF, MMG AMP, and MMG MPF were recorded during the $CP_{-10\%}$ and $CP_{+10\%}$ rides and were normalized as a percent change from the 5% timepoint of each respective ride.

Statistical analyses

Analyses were performed for the composite (defined as the mean of all of the participants) $\dot{V}O_{2peak}$, $p\dot{V}O_{2peak}$, EMG AMP, EMG MPF, MMG AMP, and MMG MPF responses during the exhaustive rides at $CP_{-10\%}$ and $CP_{+10\%}$. Separate one-way repeated measures ANOVAs with post-hoc Bonferroni corrected pairwise comparisons were used to determine if there were differences in $\dot{V}O_{2peak}$ and $p\dot{V}O_{2peak}$ among the GXT, $CP_{-10\%}$ and $CP_{+10\%}$ rides to exhaustion. The neuromuscular responses were normalized to observe the pattern of responses over time. The EMG AMP, EMG MPF, MMG AMP, and MMG MPF were normalized as a percent change from the initial 5% timepoint for each respective ride to exhaustion. Time was normalized as a percentage of the T_{lim} to account for the differences in times to exhaustion among the participants[10] and 11 data points were used in the analyses (5, 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100 % of T_{lim}). The first 5% of EMG and MMG signals was omitted from analyses to account for changes in neuromuscular activity as the participant adjusted to pedal cadence[22,38]. Polynomial regression analyses were used to determine the composite normalized (percent change from initial 5% timepoint) EMG AMP, EMG MPF, MMG AMP, and MMG MPF responses (linear, quadratic, or cubic) versus $\%T_{lim}$ (5-100%) during rides at $CP_{-10\%}$ and CP_{+10}. Separate one-way repeated measures ANOVA 1 (neuromuscular measurement (EMG AMP, EMG MPF, MMG AMP, MMG MPF)) x 11 (% of ride to exhaustion (5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100) were used to identify time course of changes in the composite, normalized neuromuscular measurements. Post-hoc Student Newman-Keuls tests were then used to determine the time course of changes among the repeated measured variables[22,25]. The Student Newman-Keuls analysis was used to examine the difference in the onset of neuromuscular fatigue between rides to exhaustion at $CP_{-10\%}$ and $CP_{+10\%}$. The analyses were conducted using Statistical Package for the Social Sciences software (v.21.0. IMB SPSS Inc., Chicago, Illinois, USA) and an alpha level of $p \leq 0.05$ was considered statistically significant.

Table 1. Means (± SD) for the power output associated with $\dot{V}O_{2peak}$ ($p\dot{V}O_{2peak}$) (W) during the graded exercise test to exhaustion (GXT) as well as the power output (W) and time to exhaustion (T_{lim}) during the continuous, constant power output rides at 10% below ($CP_{-10\%}$) and 10% above critical power ($CP_{+10\%}$).

	$\dot{V}O_{2peak}$ (L·min^{-1})	$p\dot{V}O_{2peak}$ (W)
GXT	3.39 ± 1.05	256 ± 66
$CP_{-10\%}$	3.03 ± 1.02*^	191 ± 60*^
$CP_{+10\%}$	3.39 ± 1.14	232 ± 73*

**Indicates significantly different than the GXT at a Bonferroni corrected alpha level p≤0.017*
^Indicates $CP_{-10\%}$ was significantly different than $CP_{+10\%}$ at a Bonferroni corrected alpha level of p≤0.017.

Results

Table 1 provides the mean (± SD) for $p\dot{V}O_{2peak}$ (W) and $\dot{V}O_{2peak}$ for the GXT as well as the power outputs (W) and $\dot{V}O_2$ values at exhaustion for $CP_{-10\%}$, and $CP_{+10\%}$. The power output at $CP_{-10\%}$ (74 ± 7.1% of $p\dot{V}O_{2peak}$) was significantly lower than $CP_{+10\%}$ (90 ± 9% of $p\dot{V}O_{2peak}$) ($p<0.001$), and both $CP_{-10\%}$ ($p<0.001$) and CP_{+10} ($p=0.010$) reflected a lower power output than $p\dot{V}O_{2peak}$ (Table 1). The $\dot{V}O_2$ at exhaustion for the rides at $CP_{-10\%}$ was lower than $\dot{V}O_{2peak}$ ($p=0.006$) and $CP_{+10\%}$ ($p=0.001$). The $\dot{V}O_2$ at exhaustion for the rides at $CP_{+10\%}$ was not different from $\dot{V}O_{2peak}$ ($p=1.00$) (Table 1). The T_{lim} values for the continues rides to exhaustion at $CP_{-10\%}$, and $CP_{+10\%}$ were 23.92 ± 9.42 min and 7.41 ± 4.18 min, respectively.

Figure 1 shows the results of the polynomial regression analyses and one-way repeated measure ANOVAs with post-hoc Student Newman-Keuls test for the normalized (percent change from 5% timepoint) EMG AMP, EMG MPF, MMG AMP, and MMG MPF vs. time relationship during rides to exhaustion at $CP_{-10\%}$. The one-way repeated measures ANOVAs indicated there were significant differences among timepoints for EMG AMP ($F=4.013$, $p\eta^2=0.286$, $p<0.001$) and MMG AMP ($F=3.454$, $p\eta^2 = 0.257$, $p=0.001$), and no significant differences among timepoints for EMG MPF ($F=1.617$, $p\eta^2= 0.139$, $p=0.112$) and MMG MPF ($F=1.774$, $p\eta^2= 0.151$, $p=0.075$). There was a significant positive linear relationship ($r^2=0.756$, $p=0.001$) for EMG AMP and a cubic relationship ($R^2=0.951$, $p=0.020$) for MMG AMP, that both significantly increased from the initial 5% timepoint at 100% of the ride to exhaustion. There was a significant quadratic relationship for EMG MPF ($R^2=0.678$, $p=0.015$) and MMG MPF ($R^2=0.837$, $p=0.001$) during the ride to exhaustion, with no significant differences between any of the timepoints and the initial 5% timepoint.

Figure 2 shows the results of the polynomial regression analyses and one-way repeated measure ANOVAs with post-hoc Student Newman-Keuls test for the normalized

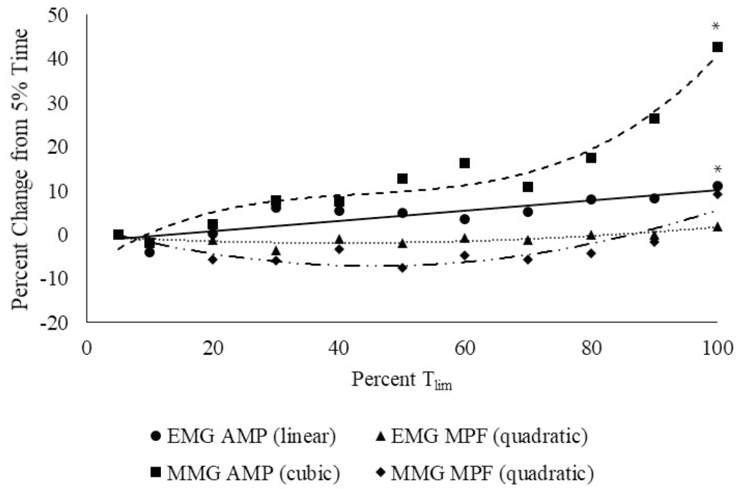

Figure 1. Time course of changes in electromyographic (EMG) and mechanomyographic (MMG) amplitude (AMP) and mean power frequency (MPF) during rides to exhaustion at 10% below critical power. The EMG and MMG signals were normalized as a percent change from the 5% timepoint and time was normalized as a percent of the time to exhaustion (T_{lim}). The x-axis crosses the y-axis at -20%. *(*Indicates starting and ending of significant difference from the initial 5% timepoint. • EMG AMP: significantly greater than 5% timepoint at 100% of ride to exhaustion only. ■ MMG AMP: significantly greater than 5% timepoint at 100% of ride to exhaustion only).*

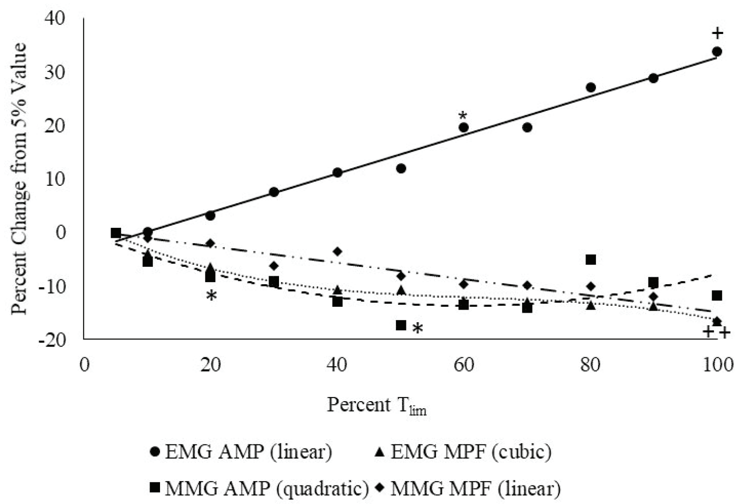

Figure 2. Time course of changes in electromyographic (EMG) and mechanomyographic (MMG) amplitude (AMP) and mean power frequency (MPF) during rides to exhaustion at 10% above critical power. The EMG and MMG signals were normalized as a percent change from the 5% timepoint and time was normalized as a percent of the time to exhaustion (T_{lim}). The x-axis crosses the y-axis at -20%. *(*Indicates starting of significant difference from the initial 5% timepoint. +Indicates ending of significant difference from the initial 5% timepoint. • EMG AMP: significantly greater than 5% timepoint from 60-100% of ride to exhaustion. ▲ EMG MPF: significantly less than 5% timepoint from 20-100% of ride to exhaustion. ■ MMG AMP: significantly less than 5% timepoint at only 50% of ride to exhaustion. ◆ MMG MPF: significantly less than 5% timepoint at only 100% of ride to exhaustion).*

(percent change from 5% timepoint) EMG AMP, EMG MPF, MMG AMP, and MMG MPF vs. time relationship during the continuous rides to exhaustion at $CP_{+10\%}$. The one-way repeated measures ANOVAs indicated there were significant differences among timepoints for EMG AMP (F = 15.404, $p\eta^2$=0.606, p<0.001), EMG MPF (F=12.344, $p\eta^2$=0.552, p<0.001), MMG AMP (F= 2.166, $p\eta^2$=0.178, p=0.026), and MMG MPF (F=3.699, $p\eta^2$= 0.270, p<0.001). There was a significant positive linear relationship (r^2=0.985, p<0.001) for EMG AMP that began to significantly increase from the initial 5% timepoint at 60% and continued to 100% of the ride to exhaustion. The EMG MPF resulted in a cubic relationship (R^2=0.986, p=0.002) that began to significantly decrease from the initial 5% timepoint at 20% and continued to 100% of the ride to exhaustion. There was a significant quadratic relationship (R^2=0.567, p=0.037) in MMG AMP during the ride to exhaustion, which significantly decreased from the initial 5% timepoint at only the 50% timepoint. The MMG MPF resulted in a significant negative linear relationship (r^2=0.932; p<0.001) that significantly decreased from the initial 5% timepoint at 100% of the ride to exhaustion.

Discussion

The present study examined the time course of changes in neuromuscular responses during rides to exhaustion at power outputs below ($CP_{-10\%}$) and above ($CP_{+10\%}$) CP. Theoretically, CP reflects the demarcation of the heavy and severe intensity exercise domains[4]. Within the heavy intensity exercise domain, $\dot{V}O_2$ gradually increases, but eventually reaches a steady state at a value below $\dot{V}O_{2peak}$, and T_{lim} is between 30 and 60 minutes[4,6]. Within the severe intensity domain, $\dot{V}O_2$ is driven to its peak value, and T_{lim} occurs within ~20 minutes[4,6]. There is conflicting evidence, however, regarding the accuracy of the CP model for estimating the highest sustainable (30-60 min) intensity[39,40]. Previous studies have demonstrated that the CP model may overestimate the highest sustainable intensity by a minimum of 15%[39,40] and may result in metabolic responses that do not reach steady state[41,42]. In the present study, the rides at $CP_{-10\%}$ and $CP_{+10\%}$ resulted in T_{lim} values of 23.92 ± 9.42 min and 7.41 ± 4.18 min, respectively. Although $\dot{V}O_2$ at exhaustion during the ride at $CP_{-10\%}$ did not reach $\dot{V}O_{2peak}$ (~89%), the T_{lim} indicated CP may have been overestimated, resulting in rides at $CP_{-10\%}$ that were performed in the severe intensity exercise domain. Previous studies[42,43] have proposed two intensity zones within the severe domain, a lower zone, where $\dot{V}O_2$ does not reach $\dot{V}O_{2peak}$, and an upper zone, where $\dot{V}O_2$ is driven to $\dot{V}O_{2peak}$. Thus, it is possible the rides at $CP_{-10\%}$ were performed in the lower zone of the severe intensity exercise domain, while those at $CP_{+10\%}$ were performed in the upper zone.

In the present study, EMG and MMG AMP increased over time during the $CP_{-10\%}$ ride and were significantly greater than the initial 5% timepoint at 100% T_{lim}. The increase in EMG AMP across time was consistent with the EMG AMP responses previously reported for continuous, exhaustive cycle ergometry performed at intensities between 50 and 90% peak power[8,10] and may have reflected fatigue-induced increases in muscle activation to maintain force production. Furthermore, the increase in MMG AMP over time suggested the increased muscle activation (EMG AMP) was likely related to recruitment of additional motor units[20]. Previous studies have reported increases, decreases, or no change in MMG AMP during cycle ergometry to exhaustion, indicating there may be intensity (50-95% peak power) and duration (11 to 60 min) as well as muscle specific responses (vastus lateralis versus vastus medialis) for MMG AMP[3,9,10].

Although there were no significant differences between any timepoints and the initial 5% timepoints, there were quadratic relationships for EMG and MMG MPF over time during the $CP_{-10\%}$ ride. The quadratic relationship of both signals reflected an initial trend toward a decline from baseline until 50% T_{lim} and a gradual return to baseline from 50% to 100% T_{lim} (Figure 1). For MMG MPF, the initial steady decline and gradual return to baseline during the latter half of the ride suggested a decrease, followed by an increase in the global motor unit firing rate[20]. In contrast to the findings of the current study, continuous (81 ± 6% peak power) and incremental (+30 Watts every 2 min until exhaustion) cycle ergometry work bouts have resulted in either a decrease or no change in MMG MPF[9,44], respectively, indicating differences in MMG MPF responses that are dependent on the intensity and duration of the exercise. Similarly, the quadratic nature of the EMG MPF relationship versus time suggested there may be time dependent influences of metabolic byproduct accumulation and increased muscle temperature on motor unit action potential conduction velocity (MUAP CV)[14,27,45]. Specifically, during a fatiguing work bout, the accumulation of metabolic byproducts (e.g., H^+, inorganic phosphate, ammonia, and potassium) tends to decrease MUAP CV and EMG MPF[27], while increases in muscle temperature during prolonged exercise (>10 minutes) have been shown to increase EMG MPF[45]. Consequently, these competing influences may have resulted in the quadratic relationship for EMG MPF during the ride at $CP_{-10\%}$. Thus, the current findings indicated increases in muscle activation and motor unit recruitment (EMG and MMG AMP), while the quadratic relationships for EMG MPF and MMG MPF may suggest fatigue-induced changes in MUAP CV and time dependent changes in motor unit activation strategies, respectively.

The neuromuscular responses (EMG and MMG AMP and MMG MPF) observed during the ride to exhaustion within the lower zone of the severe intensity exercise domain ($CP_{-10\%}$) (74 ± 7% p$\dot{V}O_{2peak}$) were consistent with the Onion Skin Scheme[11,26] and Muscular Wisdom[13] motor unit activation strategies, but not the after-hyperpolarization strategy which suggests increases in both amplitude and frequency[12]. Specifically, the Onion Skin Scheme suggests there are fatigue-induced increases in EMG AMP (muscle activation) and MMG AMP (motor unit recruitment) and decreases in MMG MPF (motor unit firing rate) due to the recruitment of higher threshold motor units that have lower firing rates than previously activated motor units[11,26]. Thus, the ride at $CP_{-10\%}$ in the present study resembles the Onion Skin Scheme motor unit activation strategy as the increases in EMG AMP and MMG AMP suggested increases in motor unit recruitment, while the quadratic MMG MPF response may have reflected the competing influences of lower firing rates of the newly recruited motor units and increases in firing rates of the already activated motor units on the average or global motor unit firing rate. Muscular Wisdom is also characterized by increases in EMG and MMG AMP (muscle activation and motor unit recruitment, respectively) and decreases in MMG MPF (motor unit firing rate)[13], which are attributed to a decrease in relaxation time of the whole muscle and in motor unit firing rate, thus providing greater twitch fusion and an economical activation of previously recruited motor units[13,27]. Therefore, the decrease in the MMG MPF could be attributed to motor unit synchronization[13,27] proposed by the Muscular Wisdom model, while the increase in MMG MPF towards baseline during the latter half of the $CP_{-10\%}$ ride (60% to 100% T_{lim}) may be due to competing influences of increased muscle stiffness (increases MMG MPF)[20]. Further examination of the motor unit action potentials and their firing rates as well as the mechanical properties of the muscle may help identify the motor unit activation strategy behind the quadric nature of the MMG MPF relationship during the ride at $CP_{-10\%}$.

The steady increase in EMG AMP and MMG AMP and significantly greater response observed at 100% T_{lim} indicated neuromuscular fatigue during the $CP_{-10\%}$ ride. These findings suggested CP obtained from the 3-min all out test may overestimate the highest intensity that can be maintained without fatigue and supports the hypothesis that the $CP_{-10\%}$ ride to exhaustion was performed in the lower zone of the severe intensity exercise domain[43]. These findings were consistent with previous research indicating an overestimation of CP estimated from the 3-min all out test[8,9,29]. Furthermore, the increases in muscle activation (EMG AMP) and motor unit recruitment (MMG AMP), along with time dependent changes in motor unit firing rate (MMG MPF) suggested the Onion Skin Scheme[11] and/or Muscular Wisdom[13] could explain the motor unit activation strategy used to maintain power output throughout the fatiguing ride at $CP_{-10\%}$.

During the ride at $CP_{+10\%}$, EMG AMP (muscle activation) significantly increased over time, while MMG AMP (motor unit recruitment) displayed a quadratic relationship that reflected an initial decrease from baseline that was significantly less than the initial 5% timepoint at 50% T_{lim} and a gradual return to baseline from 50% to 100% T_{lim} (Figure 2). The increase in EMG AMP across time is consistent with previous literature that has also reported increases in muscle activation (EMG AMP) during continuous cycle rides performed at CP (78 ± 7%) and at intensities ranging from 50-95% peak power[8,10]. Previous evidence, however, has demonstrated duration, power output, and muscle dependent responses of the MMG AMP signal. Specifically, increases, decreases, or no change in MMG AMP have been reported with varying power outputs (28-95% peak power), T_{lim} (4 to 60 min) and muscle recorded (vastus lateralis or vastus medialis)[3,9,10,46]. Furthermore, the quadratic nature of the MMG AMP relationship in the present study may be related to competing influences of decreased muscular compliance (i.e. intramuscular pressure, which can decrease MMG AMP) and increased motor unit recruitment (which can increase MMG AMP)[20]. Increases in intramuscular pressure have been reported during the first 50% T_{lim} during fatiguing isometric contraction of the leg extensors[47]. In addition, previous studies[23,24] have reported cubic responses for MMG AMP during fatiguing exercise that were hypothesized to be related to the competing influences of intramuscular pressure and motor unit recruitment. Thus, it is possible in the present study, increased intramuscular pressure during the ride at $CP_{+10\%}$ (90 ± 9% p$\dot{V}O_{2peak}$) resulted in an attenuation of the lateral oscillations of the muscle fiber that offset the effects of increased motor unit recruitment and resulted in a decrease in MMG AMP[20,46] during the first 50% of the ride (Figure 2), while the increase in MMG AMP in the latter half of the ride suggested an increase in motor unit recruitment affected the signal to a greater extent than increased intramuscular pressure[10]. Therefore, it is likely the competing influences of increased motor unit recruitment and intramuscular pressure led to the observed quadratic relationship in MMG AMP during the ride at $CP_{+10\%}$.

Both EMG MPF (MUAP CV) and MMG MPF (motor unit firing rate) decreased throughout the ride to exhaustion performed at $CP_{+10\%}$ and were significantly less than the initial 5% timepoint at 20% T_{lim} and 100% T_{lim}, respectively. Decreases in EMG MPF are associated with the accumulation of metabolic byproducts (e.g., H^+, inorganic phosphate, ammonia, and potassium), which can decrease the MUAP CV[27]. Specifically, an accumulation of potassium ions and a depletion of sodium ions can decrease the excitability of the muscle membrane and consequently decrease the MUAP CV (EMG MPF)[27]. This is consistent with previous research during rides to exhaustion lasting 10 to 80 min performed at power outputs corresponding to 78 ± 7% peak power and 60-80% $\dot{V}O_{2max}$[8,45]. A decrease in MMG MPF, however, can be attributed to a decrease in the global motor unit firing rate, due to recruitment of higher threshold motor units with lower firing rates[11,26] or the economical activation of motor units[13]. While the MMG AMP response appears to be affected by an increase in intramuscular pressure (decrease at the start of the ride), the MMG MPF signal may have been more affected by the decrease in global motor unit firing rate throughout the ride at $CP_{+10\%}$. Thus, the neuromuscular responses at $CP_{+10\%}$ suggest a similar motor unit activation strategy as that in the ride at $CP_{-10\%}$, with different competing influences affecting the nature of the responses.

The Onion Skin Scheme[11,26] and Muscular Wisdom[13] motor unit activation strategies, and not the after-hyperpolarization theory[12], best explain the neuromuscular responses observed during rides to exhaustion performed within the upper zone of the severe intensity exercise domain ($CP_{+10\%}$). The Onion Skin Scheme and Muscular Wisdom motor unit activation strategies are characterized by increases in EMG and MMG AMP and decreases in MMG MPF. During the ride at $CP_{+10\%}$, EMG AMP increased linearly throughout the entire ride to exhaustion, and showed a marked increase at 60% T_{lim}. This likely indicated an increase in motor unit recruitment, as the significant increase in EMG AMP (60% T_{lim}) coincided with the trend towards an increase observed in MMG AMP (60% T_{lim})[10]. Additionally, MMG MPF (motor unit firing rate) decreased throughout the ride to exhaustion. Although both motor control strategies are characterized by decreases in motor unit firing rate (MMG MPF), the underlying mechanisms of the decrease differ between the Onion Skin Scheme and Muscular Wisdom. More specifically, the decrease in motor unit firing rate as described by Contessa et al.[26] is due to the decrease in global motor unit firing rate from higher threshold motor units affecting the signal to a greater degree than the increasing firing rate of previously recruited motor units. This is consistent with the ride performed at $CP_{+10\%}$, as the MMG MPF did not significantly differ from the initial 5% timepoint until 100% T_{lim}, and MMG AMP (motor unit recruitment) did not begin to increase until the latter half of the ride. It is likely the lateral oscillations of the muscle fibers (MMG AMP) were attenuated during the ride at $CP_{+10\%}$ due to increased intramuscular pressure[20], thus causing the motor unit recruitment (MMG AMP) to appear to decrease, rather than increase, during the first half of the ride, and may have resulted in the nonsignificant increase during the last ~50% of the ride. Muscular Wisdom outlines the decrease in motor unit firing rate as an increase in relaxation time and decrease in motor unit firing rate, thereby allowing for synchronization of the motor units and optimized force production[13]. It is also possible the fusion of muscle twitches caused a decrease in the firing rate of recruited motor units and therefore the decrease observed in MMG MPF.

The earlier onset of changes in EMG AMP and MMG AMP and appearance of fatigue in EMG MPF and MMG MPF (indicated by timepoints significantly less than the initial 5% timepoint) during the ride at $CP_{+10\%}$, compared to $CP_{-10\%}$, suggested the ride at $CP_{+10\%}$ was performed in the upper zone of the severe intensity exercise domain[43]. Furthermore, the neuromuscular responses observed in both the $CP_{-10\%}$ and $CP_{+10\%}$ rides indicated cycle ergometry performed to exhaustion within the severe intensity exercise domain rely on motor unit activation strategies that are most closely related to the Onion Skin Scheme[11,26] and Muscular Wisdom[13] theories. Although both rides reflected similar activation strategies, the neuromuscular responses were affected by different physiological parameters (i.e., increased temperature, muscular compliance, metabolic byproduct accumulation) during rides within the lower and upper zones of the severe intensity exercise domain. This suggests exercise within the 2 zones of the severe intensity exercise domain rely on similar motor unit activation strategies to maintain power output.

Limitations of this study include the possible overestimation of CP from the 3-min all out test, which did not allow for the examination between the heavy and severe intensity exercise domains. Thus, based on the $\dot{V}O_2$ responses during rides to exhaustion at $CP_{+10\%}$ and $CP_{-10\%}$, only neuromuscular responses within the severe intensity exercise zones could be examined. Future studies should consider using a mathematical model that provides closer estimates of CP. Additionally, the analyses of neuromuscular fatigue during rides performed above CP ($CP_{+10\%}$) versus below CP ($CP_{-10\%}$) examined a combined sample of men and women. Future studies should compare the time course of changes in neuromuscular responses between men and women to determine if there are sex differences in the onset of fatigue during cycle ergometry above and below CP.

Acknowledgements

TKD was a substantial contributor to data acquisition, analysis, and interpretation, and drafting the manuscript, was the primary author, and takes responsibility for the integrity of the data analysis. MTB helped carry out data analysis and interpretation. KCS and NDMJ helped with data acquisition, analysis, and interpretation of the data. TJH, RJS, and GOH were substantial contributors to the conception and design of the work and data analysis and interpretation. HCB was the primary manuscript revisor, contributed to the conception and design of the work, and carried out data acquisition, analysis, and interpretation. All authors contributed to revising the work and approved the final submission of this manuscript.

There were no sources of external funding for this work.

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