Muscle Coordination Limits Efficiency and Power Output of Human Limb Movement under a Wide Range of Mechanical Demands

Ollie M. Blake¹ and James M. Wakeling¹

¹Department of Biomedical Physiology and Kinesiology, Simon Fraser University, Burnaby, British Columbia, Canada

Corresponding author: Ollie M. Blake
Department of Biomedical Physiology & Kinesiology, Simon Fraser University, 8888 University Drive, Burnaby, BC, Canada V5A1S6
Phone: 778-782-8445
Fax: 778-782-3040
Email: omb@sfu.ca

Running Title: Muscle Coordination Limits Movement Efficiency & Power
Abstract

This study investigated the influence of cycle frequency and workload on muscle coordination and the ensuing relationship with mechanical efficiency and power output of human limb movement. Eleven trained cyclists completed an array of cycle frequency (cadence)-power output conditions while excitation from 10 leg muscles and power output were recorded. Mechanical efficiency was maximized at increasing cadences for increasing power outputs and corresponded to muscle coordination and muscle fibre type recruitment that minimized both the total muscle excitation across all muscles and the ineffective pedal forces. Also, maximum efficiency was characterized by muscle coordination at the top and bottom of the pedal cycle and progressive excitation through the uniarticulate knee, hip and ankle muscles. Inefficiencies were characterized by excessive excitation of bi-articulate muscles and larger duty cycles. Power output and efficiency were limited by the duration of muscle excitation beyond a critical cadence (120-140 r.p.m.) with larger duty cycles and disproportionate increases in muscle excitation suggesting deteriorating muscle coordination and limitations of the activation-deactivation capabilities. Most muscles displayed systematic phase shifts of the muscle excitation relative to the pedal cycle that were dependent on cadence and to a lesser extent power output. Phase shifts were different for each muscle thereby altering their mechanical contribution to the pedaling action.

This study shows that muscle coordination is a key determinant of mechanical efficiency and power output of limb movement across a wide range of mechanical demands and that the excitation and coordination of the muscles is limited at very high cycle frequencies.

Key Words
Electromyography, Excitation, Power output, Cadence, Cycling, Motor Control
Introduction

Human limb movement is achieved through interactions between the neuromuscular and skeletal systems. Movement performance is commonly measured by the resultant mechanical efficiency (ratio of mechanical power output to metabolic power) and power output, both of which are significantly influenced by the coordinated excitation of individual muscles and the coordination of that excitation between muscles (Blake et al., 2012; Dorel et al., 2012; Samozino et al., 2007; Wakeling et al., 2010). Therefore, investigating movement performance requires a comprehensive understanding of how the individual muscle excitations and the coordination between muscles (muscle coordination) change in response to the demands.

Mechanical demands such as workload and movement velocity can be uncoupled during cycling (Wakeling et al., 2006; Wakeling and Horn, 2009) making it an appropriate model to investigate the effects of mechanical demands on individual muscle excitation and muscle coordination and the resultant performance outcomes. First, the relative excitation of each muscle is both workload (Blake et al., 2012; Blake and Wakeling, 2012, 2013; Ericson, 1986; Ericson et al., 1985; Hug et al., 2004; Jorge and Hull, 1986; Sarre et al., 2003; Wakeling et al., 2010; Wakeling and Horn, 2009) and cadence dependent, with many discrepancies in the collective research (Ericson, 1986; Ericson et al., 1985; Lucia et al., 2004; Neptune et al., 1997, 1997; Sarre et al., 2003; Sarre and Lepers, 2005, 2007; Takaishi et al., 1996, 1998; Wakeling et al., 2006; Wakeling and Horn, 2009). Evidence suggests that individual muscles exhibit workload dependent relationships between muscle excitation and cadence (MacIntosh et al., 2000), which may explain the discrepancies as a wide range of workloads were employed. The timing of muscle excitation has also been shown to be affected by cadence,
with several muscles exhibiting a phase advance and/or larger duty cycle with increasing cadence (Baum and Li, 2003; Dorel et al., 2012; Marsh and Martin, 1995; Neptune et al., 1997; Samozino et al., 2007; Sarre and Lepers, 2005, 2007; Wakeling and Horn, 2009), and both influenced (Sarre and Lepers, 2007) and not influenced (Jorge and Hull, 1986) by workload, but relatively little research has been completed in this area.

The influence of workload and cadence on muscle coordination is important as muscle coordination impacts mechanical efficiency (Blake et al., 2012; Wakeling et al., 2010) and power output (Dorel et al., 2012; Samozino et al., 2007; Wakeling et al., 2010), yet few studies have looked at the spatiotemporal muscle excitation-workload-cadence relationships across multiple muscles. Efficiency in cycling has been reviewed (Ettema and Loras, 2009) and has been shown to be dependent largely on workload and to a lesser extent on cadence, while delta efficiency (ratio of the change in mechanical power to the change in metabolic power) has been shown to be independent of workload (Hansen and Sjogaard, 2007) and both independent (Marsh et al., 2000) and dependent on cadence (Böning et al., 1984; Chavarren and Calbet, 1999; Sidossis et al., 1992). If delta efficiency increases with cadence (Böning et al., 1984; Chavarren and Calbet, 1999) then an increase in power output requires less energy at higher cadences compared to lower cadences (Sargeant and Beelen, 1993). This partially explains evidence that efficiency is maximized at increasing cadences for increasing power outputs (Böning et al., 1984; Coast and Welch, 1985; Foss and Hallén, 2004; Hagberg et al., 1981; Seabury et al., 1977). Obtaining greater efficiency by increasing cadence with workload may be the result of reduced muscle excitation since minimum muscle excitation also occurs at increasing cadences with increasing submaximal workloads (MacIntosh et al., 2000), despite different muscle excitation-workload-cadence relationships seen in individual muscles.
Maximum mechanical efficiency occurs at cadences below the optimal cadences reached at maximum power output and so there is a trade-off between efficiency and power in cycling (Kohler and Boutellier, 2005) that has been linked to differences in muscle coordination (Blake et al., 2012). Maximum efficiency in cycling has been predicted to occur at approximately 50 revolutions per minute (r.p.m.) and 150 r.p.m. in slow and fast muscle fibres, respectively, and therefore at an intermediate cadence in a mixed fibre type muscle (Sargeant, 2007). Thus-increasing cadence with power output to maximize efficiency may reflect the need for the additionally recruited faster muscle fibres to operate at higher velocities to maximize their efficiencies (Sargeant and Beelen, 1993). Greater relative recruitment of fast muscle fibres at 50 r.p.m. compared to 100 r.p.m. at approximately 335 W (Ahlquist et al., 1992) supports this idea since more fast fibres would be necessary at 50 r.p.m. to make up for their inability to effectively produce power at low velocities. In addition, faster muscle fibres are recruited at high cycle frequencies, such as 120 r.p.m., at high and low workloads (Farina et al., 2004), which may be to compensate for the inability of slow fibres to effectively produce power at high velocities (Sargeant, 1994; Sargeant and Beelen, 1993). Finally, maximum power output in cycling occurs at 110-120 r.p.m. (Beelen and Sargeant, 1991; Dorel et al., 2010; Hautier et al., 1996; Samozino et al., 2007; Sargeant et al., 1981) where faster muscle fibres have a greater contribution to maximum power output at higher cadences such as those found at 120 r.p.m. (Beelen and Sargeant, 1991). The mechanical efficiency and power output of limb movement are significantly influenced by muscle coordination, (Blake et al., 2012; Dorel et al., 2012; Samozino et al., 2007;
Wakeling et al., 2010), which is affected by the mechanical demands of the movement. Little is known about the mechanical demand and muscle coordination relationships or their subsequent influence on mechanical efficiency and power output. Therefore, the objectives of this study were to map the muscle coordination of ten leg muscles across a wide range of mechanical demands to: 1) determine if individual muscle excitation responses to changes in cadence are workload dependent and 2) determine if critical cadences exist where distinct changes in individual muscle excitation and muscle coordination can be identified that coincide with maximum efficiencies and maximum power output. It was hypothesized that an interactive influence of cadence and workload on muscle excitation exists that will explain previous inconsistencies in the literature with respect to muscle excitation responses to different demands. It was also hypothesized that distinct shifts in muscle coordination and muscle fibre recruitment would coincide with maximum efficiency and this would be demonstrated by shifts in the relative timing and amplitude of the EMG intensity and frequency content of the EMG signal.

Methods

Protocol and Data Acquisition

Eleven competitively trained male cyclists (mean ± s.e.m.: age = 33.9 ± 3.1 years, mass = 72.8 ± 2.1 kg, height = 179.1 ± 1.9 cm, cycling distance per year = 10773 ± 1575 km) volunteered to participate in the study. Trained cyclists were necessary in order to successfully complete the extreme cycling conditions of the testing protocol. All participants gave their informed written consent to participate and the ethics committee in accordance with the Office of Research Ethics at Simon Fraser University approved all procedures.
The participants cycled at cadences of 40, 60, 80, 100, 120, 140, 160 and 180 r.p.m. at each of 100, 200, 300 and 400 W on an indoor cycle trainer (Schoberer Rad Messtechnik (SRM), Julich, Germany). The participants completed a 10-minute warm-up at a freely chosen cadence with 5 minutes at 100 W followed by 5 minutes increasing 20 W each minute. The conditions were first randomized by cadence and then each power output was presented in random order to help ensure compliance of the desired cadence (MacIntosh 2000). The geometry of the cycle trainer was matched to each participant’s own bicycle as closely as possible, and they used their own clipless pedals and shoes. Cyclists were instructed to maintain a seated position with hands on the brake hoods while data were collected and each trial was 30 seconds in duration with 90 seconds rest between.

Electromyographic (EMG) signals were recorded continuously from 10 muscles of the right leg (tibialis anterior (TA), MG, LG, Sol, vastus medialis (VM), rectus femoris (RF), vastus lateralis (VL), semitendinosus (ST), biceps femoris (BF) and gluteus maximus (GM)) using bipolar Ag/AgCl surface electrodes with 10 mm diameter and 21 mm spacing (Norotrode; Myotronics, Kent, WA). The skin of the right leg in the location of the electrodes was prepared by removing hair and dead skin and cleaning with isopropyl wipes. The electrodes were fixed to the skin with stretchable adhesive bandages and the entire leg was covered with a tubular net bandage to reduce movement artifacts. The EMG signals were amplified (gain 1000), band-pass filtered (bandwidth 10-500 Hz: Biovision, Wehrheim, Germany) and recorded at 2000 Hz (16-bit analog to digital converter: USB-6210; National Instruments, Austin, TX). Cadence and the effective (normal) and ineffective (tangential) forces applied to the crank arms were recorded using instrumented pedals (Powerforce, Radlabor, Freiburg,
Germany) simultaneously with the EMG. Crank forces were subsequently used to calculate power output.

**Data Analysis**

The EMG signals were resolved into intensities in both time and frequency space using an EMG-specific wavelet analysis where EMG intensity is similar to the power of the EMG signal (von Tscharner, 2000). The wavelets had a frequency bandwidth of approximately 11-432 Hz (j = 1-10; (von Tscharner, 2000). EMG intensities for individual muscles were calculated as the sum of intensities across all ten wavelet domains for each time point. The EMG intensities were interpolated to 100 points per muscle per pedal cycle starting at top dead center of the right crank arm rotation and were normalized to the mean for each muscle for each participant across all trials. The total EMG intensity was calculated for each muscle and pedal cycle as the sum of the interpolated intensities. From each 30 second trial, only data from the first five pedal cycles within five r.p.m. of the desired cadence and within 10% of steady-state power output were retained for further analysis.

Principal Component (PC) Analysis was used to determine the primary muscle coordination patterns across a pedal cycle. PC analysis has been increasingly used as a method for muscle coordination analysis (Blake et al., 2012; Blake and Wakeling, 2012; Enders et al., 2014; Wakeling et al., 2010; Wakeling and Horn, 2009). It is a valuable tool for the reduction of large multivariate data sets making it useful for muscle coordination during repetitive actions such as cycling to identify common underlying features. In addition to PC analysis, other data reduction tools, such as non-negative matrix factorization, have been utilized to investigate muscle coordination during cycling (Barroso et al., 2014; De Marchis et al., 2013; Hug et al.,
2010), although these have been focused on data reduction with respect to muscle synergies. In this study we were not attempting to describe muscle synergies and used PC analysis as it provided the opportunity to extract sources of variability related to specific outcomes while allowing for negative values. Negative values in the PCs were important as they allowed for the possibilities of signal reductions as might be expected by inhibitory control signals in muscle excitation. Muscle coordination patterns were extracted using the interpolated EMG intensities (100 points per muscle per pedal cycle) as has been described previously (Blake et al., 2012; Blake and Wakeling, 2012; Wakeling and Horn, 2009). In order to visualize the primary differences in muscle coordination for each condition, EMG intensities were reconstructed from the vector sum of the muscle coordination PC’s (PC_{mus}) weightings and loading scores for the first 10 principal components (Blake et al., 2012).

Muscle bursts were extracted (using an onset/offset threshold of 5% of the difference between the maximum and minimum EMG intensity: (Blake and Wakeling, 2014) and the burst duration and duty cycle (proportion of muscle excitation relative to a complete pedal cycle) were calculated for each muscle for each pedal cycle. For each muscle burst the EMG intensities were interpolated to 100 points for each wavelet (10 wavelets * 100 points = 1000 points per muscle burst) and normalized to the maximum intensity across all wavelets for each muscle for each participant across all trials. The time-frequency patterns were quantified from the interpolated frequency spectra (100 points per muscle per wavelet per muscle burst) using a Principal Component analysis (Blake and Wakeling, 2014). The first time-frequency PC (PC_{freq1}) approximated the mean time-varying frequency spectra with subsequent PC_{freq}’s representing the variation in time and frequency from PC_{freq1}. The second and third PC_{freq}’s (PC_{freq2} and PC_{freq3}) showed distinct shifts in EMG intensity at different times and
frequencies within each muscle burst and were therefore used to calculate vectors in PCfreq3-
PCfreq2 space using the mean loading scores for each condition. A change in the direction of
these vectors for different conditions represents a change in the time-varying frequency of the
EMG intensity for each muscle burst.

Relative phase shifts of the EMG intensities for each muscle across a pedal cycle were
determined using the Procrustes shift registration method (Ramsay and Silverman, 2005).
These were determined separately for cadence and power output by analyzing the shift due to
cadence at each power output and the shift due to power output at each cadence. Phase shifts
due to cadence and power output were also calculated in a similar manner for the effective,
ineffective and resultant pedal forces. Relationships between the mean pedal force per pedal
cycle and cadence were determined at each power output for the effective, ineffective and
resultant pedal forces. Where a parabolic relationship was evident a best-fit 2nd or 3rd order
polynomial was determined for the data using a linear least-squares fit (Mathematica Version
10, Wolfram Research, Inc., Champaign, USA) to estimate the cadence at which minimum
pedal forces occurred. The relative efficiency was estimated as the ratio of mechanical power
output measured at the pedals to the sum of the total EMG intensities across all muscles
where total EMG intensity was used as a proxy for the metabolic power required for cycling
(Blake and Wakeling, 2013; Wakeling et al., 2011). The relationships between cadence and
both efficiency and total EMG intensity across all muscles were determined at each pedal
cycle and best-fit polynomials were fit to the data to estimate the cadence at which efficiency
was maximized and total EMG intensity was minimized.

In order to mitigate any effects of fatigue on the EMG signals the randomized block design
was implemented. Also, to evaluate the presence of fatigue additional 30 second trials were
completed, at the same cadence as the first trial at 200 W, prior to the 1st, 17th and after the last trial (MacIntosh et al., 2000) where an increase in EMG intensity was expected where fatigue was present (Edwards and Lippold, 1956; Housh et al., 2000; Petrofsky, 1979; Sarre and Lepers, 2005).

Statistics

The influence of power, cadence and any interaction between power and cadence on muscle coordination was determined using general linear model analyses of variance (ANOVA) using each of the first 20 muscle coordination PC’s (PCmus loading scores) individually as the dependent variable and subject as a random factor. This same analysis was also completed for the first 10 PCfreq’s for each muscle. The effects of cadence and power output on EMG intensity, total EMG intensity across all muscles, efficiency, muscle burst duration and duty cycle, mean effective, ineffective and resultant pedal forces and pedal force and EMG intensity phase shifts were evaluated using one-way ANOVAs. Where significant effects were found, Tukey’s post hoc tests were performed to determine differences between cadences for a particular power output, when cadence was the independent variable, and between power outputs for a given cadence, when power output was the independent variable. Statistical tests were considered significant at p ≤ 0.05 and where not explicitly stated, all significances occurred at p ≤ 0.01.

Results

EMG Intensity & Muscle Coordination

The total EMG intensities and the sum of the total EMG intensities across all muscles were significantly influenced by power output, cadence and the interaction between power and
cadence (Figure 1E & Figure 2). EMG intensity of most muscles displayed an exponential relationship with cadence at low power outputs and a parabolic relationship at high power outputs increasing primarily with cadence independent of power output above 140 r.p.m. (Figure 2). As an example of the exponential relationships, there was no significant difference in the total EMG intensity between 40 and either 120 (Sol, VM and VL) or 140 r.p.m. (RF, ST, BF and GM) at 100 W and between 40 and either 120 (VL and ST) or 140 r.p.m. (Sol and GM) at 200 W. In contrast, as an example of the parabolic relationships, there was no significant difference in the total EMG intensity between 60 and 120 (ST) at 300 W and between 60 and either 120 (TA, ST and BF) or 140 r.p.m. (Sol, VM and VL) at 400 W with EMG intensities significantly larger outside these cadences (p ≤ 0.05). EMG intensity for RF and GM was not significantly different between 80 and 140 r.p.m. at 400 W thus forming a steeper parabolic relationship (Figure 2). The total EMG intensities for MG and LG increased predominantly with cadence independent of power output, while the total EMG intensities for VM, VL and BF increased primarily with power output independent of cadence below 140 r.p.m.. The total EMG intensity for TA increased with both power and cadence below 140 r.p.m..

Fatigue was evaluated by comparing total EMG intensity before the first trial, after the last trial and half way through the protocol where an increase in total EMG intensity was expected if fatigue was present. There was no significant difference between the total EMG intensity for these trials (477.08 ± 11.25, 459.89 ± 13.25 and 513.66 ± 15.08; mean ± SEM). Assessing fatigue using EMG intensity across all muscles does not provide information about changes to the individual muscles and therefore fatigue may have been present in some muscles for some subjects. The randomized block design should mitigate some of the effects of fatigue and add
variability to the processed EMG, while the inability to accurately measure fatigue presents a limitation of the interpretation of the findings.

The muscle coordination patterns for each condition can be seen in Figure 3. The first two PC$_{\text{mus}}$’s that quantify the coordination (Figure 4) explained over 66% of the variability in coordination patterns and the first ten explained over 82%. Loading scores for the first PC$_{\text{mus}}$ (PC$_{\text{mus}1}$) were significantly correlated with the sum of the total EMG intensities across all ten leg muscles ($r = 0.99$). Muscle coordination (as evaluated through the PC$_{\text{mus}}$ loading scores) had a significant effect on efficiency, with nine of the first ten PC$_{\text{mus}}$’s having an effect, while cadence and power output had significant influences on muscle coordination (Figure 4) and efficiency (Figure 1D). Muscle coordination and efficiency were also significantly affected by the interaction of cadence and power output. The predominant muscles featured in PC$_{\text{mus}2}$ to PC$_{\text{mus}5}$ were RF and GM. PC$_{\text{mus}2}$ showed a timing shift for most muscles (red occurs before blue across the pedal cycle in Figure 4), PC$_{\text{mus}3}$ highlighted a balance between RF and GM and all other muscles (different color for RF and GM compared to the other muscles in Figure 4), PC$_{\text{mus}4}$ represented the balance between RF and GM (different color for RF and GM in Figure 4) and PC$_{\text{mus}5}$ showed a shift in timing of most muscles opposite to that of RF (red occurs before blue for RF across the pedal cycle in Figure 4). Visualizations of the primary muscle coordination patterns for maximum efficiency were established through reconstructions of the EMG intensities using a reduced number of PC$_{\text{mus}}$’s. The cadence at which efficiency was maximized was 60, 76, 86 and 97 r.p.m. at 100, 200, 300 and 400 W, respectively (Figure 1D), which displayed progressive muscle excitation from the knee (VM and VL together) to the hip (GM) to the ankle (SOL) and finally to BF through the down stroke of the pedal cycle. These muscles also showed the highest levels of relative muscle
excitation for these high efficiency conditions when compared to the other muscles.

Conditions associated with decreased efficiency had the highest relative muscle excitation for RF and GM at high power outputs as well as TA, MG, LG, RF and ST across all power outputs with low relative excitation for VM and VL.

The first PCfreq (PCfreq1) of the time-varying frequency spectra explained approximately 60% of the time-frequency spectra and was similar to the mean frequency spectrum for each muscle. The loading scores for PCfreq1 were significantly correlated with each muscle’s total EMG intensity and displayed similar relationships with cadence and power output as total EMG intensity with minimum loading scores occurring at increasing cadences with increases in power outputs (Figure 1E). The first ten PCfreqs (PCfreq1 to PCfreq10) explained approximately 81-95% of the time-varying frequency spectra, depending on the muscle where PCfreq2 and PCfreq3 displayed increases and decreases in high and low frequencies and/or timing shifts of the frequency relative to the muscle burst duration (Figure 2). For example, PCfreq1 for TA was similar to the mean frequency spectrum for this muscle when time was ignored and was similar to an EMG intensity trace across a muscle burst when frequency was ignored (Figure 2). Thus the largest intensity in the muscle burst was centred at approximately 92 Hz and this occurred at approximately 50% of the burst duration. Similarly, PCfreq2 for TA showed a decrease and an increase in intensity across all frequencies before and after 50% burst duration, respectively, while PCfreq3 showed a decrease and an increase in intensity across the muscle burst below and above approximately 92 Hz, respectively (Figure 2). Vector plots showing mean loading scores of PCfreq2 and PCfreq3 projected onto plots of maximum efficiency at each condition highlight the frequency shifts of each muscle relative to cadence and power output (Figure 2). Sol, VM and VL displayed frequency shifts in PCfreq2 and
PC freq 3 that corresponded to changes in efficiency and total EMG intensity across all muscles. Notably, PC freq 1 of these muscles explained more of the time-frequency spectra for each muscle burst than any other muscle except GM. Most muscles exhibited pronounced changes in EMG frequency at the highest cadences and in some cases at 40 r.p.m..

Efficiency

Efficiency (the ratio of power output to total EMG intensity across all muscles: Blake and Wakeling, 2013; Wakeling et al., 2011) was maximized at increasing cadences for increasing power outputs from 60 r.p.m. at 100 W to 98 r.p.m. at 400 W (Figure 1D). Efficiency increased while total EMG intensity decreased at each power output (Figures 1B, 1D & 1E) with total EMG intensity displaying more pronounced parabolic relationships with cadence as power output increased (Figure 1E). Cadences for maximum efficiency (Figure 1D) coincided with cadences for minimum EMG intensity (Figure 1E) determined from the best-fit polynomials of the relationships. For example, at 400 W efficiency reached a maximum at approximately 98 r.p.m. while total EMG intensity displayed a parabolic relationship with minimum values at approximately 103 r.p.m.. The relationships between cadence, power output and efficiency can be visualized in the Figure 1D where from 40 to 80 r.p.m. efficiency decreases with each increase in power output, whereas from 100 to 180 r.p.m. it displays non-linear relationships with maximum efficiency occurring at higher power outputs as cadence increases. There was no significant difference in efficiency between 60 and 100 r.p.m. at 200 W, 60 and 120 r.p.m. at 300 W and 80 and 120 r.p.m. at 400 W.

Phase Shifts

Significant systematic phase shifts of the EMG intensity to be earlier in the pedal cycle were found with increasing cadences for all muscles ($p \leq 0.0001$ for all muscles except LG at $p = 0.0023$), yet not across all power outputs (Figure 5). Phase shifts occurred in a limited cadence range for some muscles. For example, phase shifts earlier for ST occurred primarily between 40 and 120 r.p.m. at all power outputs, while for TA, VM, VL, Sol and MG phase shifts primarily occurred from 100 to 180 r.p.m.. The largest phase shifts across the full range of cadences could be found in RF (maximum $\sim$100 degrees), ST and GM (both maxima $\sim$70 degrees) with many muscles displaying shifts of approximately 40 degrees (TA, MG, VM, VL and BF). No significant phase shift was found for the LG at 200 to 400 W, with a relatively small systematic shift at 100 W of approximately 27 degrees. Relatively small shifts were also found in Sol of approximately 20-30 degrees. The phase shifts of the EMG intensity varied with power output in muscle-specific and cadence dependent manner with the phase sometimes increasing and sometimes decreasing with power, and this is displayed in Figure 5.

**Muscle Burst Duration**

All muscles displayed a significant systematic decrease in muscle burst duration that plateaued at the highest cadences (Figure 6). There was no significant difference in muscle burst duration between 120 and 180 r.p.m. for TA (except 100 W), Sol, VM, RF, VL, ST, BF and GM (except 100 W) and between 140 and 180 r.p.m. for MG and LG. There was a significant effect of power output on burst duration for TA at 80 and 100 r.p.m., MG at 40 and 60 r.p.m. and for BF at 60 r.p.m.. Significant increases in the duty cycles were found above 120 r.p.m. for TA, Sol, VM, VL, ST (above 140 r.p.m.), BF and GM (Figure 6). No significant difference in duty cycle between cadences from 40 to 120 r.p.m. were found for TA (at 200-300 W), VM, VL, ST, BF (40 to 80 r.p.m. at 100 W) and GM (except 100 W).
There was no significant difference in duty cycle between all cadences for LG, a significant increase in duty cycle across all cadences for RF and a significant decrease in duty cycle from 40 to 100 r.p.m. at 200-400 W for Sol.

Pedal Forces

Both the peak maximum and peak minimum effective forces per pedal cycle displayed an inverse relationship with cadence across all power outputs with the differences between cadences decreasing at the highest cadences (Figure 7). Mean effective force per pedal cycle showed a decreasing relationship with cadence, whereas maximum and mean ineffective forces per pedal cycle displayed parabolic relationships with cadence with minimum values occurring at increased cadences for increased power outputs (Figure 7). All pedal forces systematically shifted later in the pedal cycle as cadence increased with the largest shifts visible in the resultant pedal force (Figure 7).

Discussion

This study investigated the influence on mechanical efficiency of cycle frequency, workload and muscle coordination across a wide range of mechanical demands. Maximum efficiency occurred at increasing cadences for increasing power outputs. Where maximum efficiency occurred it corresponded with minimum EMG intensity, minimum ineffective pedal forces, specific muscle coordination and changes in the frequency of the EMG. Therefore, the increasing cadence-power output combinations that resulted in maximum efficiencies could be identified in (1) the mechanical output, through the minimum ineffective forces; (2) in the muscle coordination patterns, with progressive muscle excitation through the uniarticulate knee, hip and ankle muscles during the down stroke; and (3) in the timing and amplitude of
different frequencies of the EMG signal in VM, VL and Sol, which provides some indication of the recruitment of different muscle fibre types (von Tscharner, 2000; Wakeling, 2009; Wakeling and Horn, 2009; Wakeling and Rozitis, 2004). Power output was also limited beyond a cycle frequency of 120-140 r.p.m. where there were plateauing muscle burst durations, longer duty cycles and disproportionate increases in EMG intensity for most muscles. These factors represented a constraint of muscle excitation, increasing metabolic costs and rapidly decreasing mechanical efficiency.

Muscle Coordination influence on Efficiency – Mechanical Demands

Efficiency was significantly affected by individual muscle excitation, muscle coordination and the mechanical demands of the cycling task. Increased efficiency at constant power output and cadence has been shown to result from a decrease in muscle excitation (EMG intensity) as a consequence of altered muscle coordination (Blake et al., 2012). The current findings add that the relationships between efficiency and both EMG intensity (Figure 1C) and muscle coordination (Figure 4) are cadence specific, with power output and cadence having an interactive influence, unifying seemingly inconsistent previous findings related to changes in EMG with cadence and power output. For example, Sarre and co-workers (2003) found RF EMG decreased with increased cadence and was higher at 60 r.p.m. than any other cadence tested (up to approximately 115 r.p.m.) at 297 and 371 W. In contrast, Ericson (1985) and Neptune (1997) determined that RF EMG was uninfluenced between 40 and 100 r.p.m. at 120 W and between 45 and 120 r.p.m. at 250 W, respectively. In the current results RF intensity displayed a parabolic relationship with cadence at high power outputs, similar to other studies (MacIntosh et al., 2000; Marsh and Martin, 1995), with the curvature decreased to an exponential relationship at 100 W (Figure 2). Therefore, RF intensity was significantly
higher at 60 r.p.m. than 100 and 120 r.p.m. at 400 W and uninfluenced between 40 and 120 r.p.m. at 100 W supporting the previous findings (Ericson et al., 1985; Neptune et al., 1997; Sarre et al., 2003). Similarly, the EMG intensity of all muscles displayed exponential and/or parabolic relationships with cadence depending on the workload (Figure 2), helping explain other differences previously found and highlighting the need to investigate a large array of conditions to fully understand individual muscle excitation and muscle coordination responses to altered mechanical demands. This research supports previous studies and the results were obtained using different methodologies, which strengthens the validity of the findings.

These results support evidence that efficiency is maximized (Böning et al., 1984; Coast and Welch, 1985; Foss and Hallén, 2004; Hagberg et al., 1981; Seabury et al., 1977) and muscle excitation is minimized (MacIntosh et al., 2000) at increasing cadences for increasing power outputs during cycling and that the influence of cadence on efficiency decreases at higher power outputs (Figure 1D; (Chavarren and Calbet, 1999; Di Prampero, 2000). Maximum efficiency occurred at 60, 76, 86 and 97 r.p.m. at 100, 200, 300 and 400 W, respectively (Figure 1D), similar to the cadences previously found for minimum muscle excitation (MacIntosh et al., 2000), and little difference in efficiency existed between all power outputs at 100 r.p.m. and between 300 and 400 W at the highest cadences. Thus a change in power output resulted in a proportionally similar change in total EMG intensity. The greatest difference in efficiency across power outputs occurred at 40 and 60 r.p.m. implying that increasing workload at low cadences required a larger increase in muscle excitation than an equal change at other cadences (Figure 1E). One explanation for increased muscle excitation at low cadences is that more faster muscle fibres would be needed to generate increased power (Ahlquist et al., 1992), however such fibres are inefficient at low shortening velocities.
Muscle Coordination influence on Efficiency – Mechanical Output

Evidence from both the muscle coordination and the resulting mechanical output, seen in the pedal forces, indicates that the top and bottom of the pedal cycle are critical to efficiently completing the cycling action (Blake et al., 2012; Dorel et al., 2010; Leirdal and Ettema, 2011), despite the effective force being low at these times (Figure 7; (Patterson et al., 1983; Sanderson, 1991). The importance of different sectors of the pedal cycle, other than the down stroke, to effectively complete the pedaling action has been shown during submaximal (Blake et al., 2012; Hug et al., 2008; Leirdal and Ettema, 2011) and maximal sprint cycling (Dorel et al., 2010; Martin and Brown, 2009; Samozino et al., 2007) and this study adds that the top and bottom are critical for efficient cycling. RF and TA were the primary muscles active at the top and MG, LG, ST and BF were the primary muscles active at the bottom of the pedal cycle, respectively (Figure 3), and all had a significant effect on efficiency (Figure 4). These muscles (except TA) are bi-articulate muscles, whereas the traditionally classified power producing muscles (VM, VL and GM) and Sol are all single joint muscles, thus supporting the notion that the bi-articulate muscles are important for the transfer of force between joints and the orientation of the forces on the pedals (Raasch et al., 1997; van Ingen Schenau et al., 1992). The ineffective pedal force displayed peak amplitudes at the top and/or bottom of the crank rotation (Figure 7), again providing evidence of the constraints and importance of these regions of the pedal cycle. The ineffective force may provide a better indication of the efficiency-cadence-workload relationships than the effective or resultant forces since there was little difference in effective force at high cadences for high workloads, making it difficult to ascertain a minimum, and the resultant force is dependent on the effective force (Figure 7).
Across all power outputs the muscle coordination patterns characteristic of maximum efficiency showed synchronized timing and progressive excitation, primarily during the down stroke, from muscles spanning the knee (VM and VL together) to the hip (GM) to the ankle (SOL) and finally to BF. In contrast, inefficient cycling was dominated by excitation of RF and GM at high power outputs, TA, MG, LG, RF and ST across most power outputs, shrinking relative levels of excitation for VM and VL and larger duty cycles for many muscles. Again, the muscles active at the top and bottom of the pedal cycle were determinants of the cycling efficiency and, while not able to conclusively ascertain, it may be speculated that the synchronized timing and progressive excitation of muscles during the down stroke may result from effective transitions at the top and bottom of the cycle.

The parabolic relationship between pedal forces and cadence (Figure 7) has been attributed to the competing requirements for decreasing muscular and increasing non-muscular components of the pedal forces with cadence, as determined from pedal force decomposition (Kautz and Hull, 1993). Beyond 90 r.p.m. the increases in pedal forces have been attributed to non-muscular components (Kautz and Hull, 1993; Neptune and Herzog, 1999), in particular the inertial component or centripetal-like force keeping the foot and leg following a constrained path (Kautz and Hull, 1993). To accommodate increased workloads at each cadence the muscular component would be higher, whereas the non-muscular components (inertial and weight) be consistent with cadence, independent of workload, since the mass of the foot and pedal, length of the crank arm and the velocity remain constant at each cadence. Therefore, it would be expected that minimum resultant and ineffective pedal forces occurred at increasing cadences for increasing power outputs (Figure 7) because the intersection of the decreasing muscular and increasing non-muscular components would depend primarily on the
muscular component. The importance of the muscular component highlights the significance of muscle activation and coordination for efficient and effective cycling action.

Muscle Excitation Timing – Limits to performance

Muscle excitation timing and burst duration were limiting factors of performance of the cyclical limb movement at high cadences. Disruptions in limb and muscle coordination occurred at consistent cadence thresholds of approximately 120-140 r.p.m. confirming the necessity to use an extreme range of cadences to investigate the limitations to produce effective and efficient movements (Samozino et al., 2007). Altered muscle coordination above 120 to 140 r.p.m. was represented in the PCmus’s where there was a reduced range of loading scores across power outputs (Figure 4). A smaller range of loading scores signifies a reduction in relative variability of the muscle coordination, which may represent a muscle coordination limit to produce these rapid movements. Muscle coordination was also affected by the plateau in muscle burst duration for all muscles beyond 120-140 r.p.m. (Figure 6), similar to previous findings for MG (Blake and Wakeling, 2014), resulting in larger duty cycles at high cadences (Figure 6). Longer muscle burst durations also limited limb movement efficiency as total EMG intensity increased disproportionately above 120-140 r.p.m. (Figure 1E) indicating a greater metabolic cost and rapidly decreasing mechanical efficiency (Figure 1D).

Evidence suggests that larger duty cycles are a limitation of the activation-deactivation dynamics of muscle resulting in increased negative muscular work and unnecessary co-contraction of antagonistic muscle pairs (Josephson, 1999; Neptune and Herzog, 1999; Neptune and Kautz, 2001; Van Soest and Casius, 2000), and this is likely to be the case for duty cycles over 50% (Figure 6). Activation-deactivation rates increase with increased
velocities (Askew and Marsh, 1998), but the extreme cadences used in this study would push the activation-deactivation capabilities. Previously, we speculated (Blake and Wakeling, 2014) that activation-deactivation limits may have been reached resulting in minimum excitation durations at the highest cadences in these mixed fibre muscles. Activation-deactivation and excitation duration limits would be particularly impactful during the extension-flexion transitions of the hip, knee and ankle at the top and bottom of the pedal cycle since deactivation would need to occur over a shorter portion of the pedal cycle to apply force long enough for the task and not induce large amounts of negative muscular work.

The muscles did not apply force at the same location of the pedal cycle as the mechanical demands changed, effectively altering their mechanical contribution to the performance of the limb movement (Samozino et al., 2007). For example, VM and VL shifted their excitation earlier in the pedal cycle by approximately 40 degrees, most of which occurred above 120-140 r.p.m. (Figure 3 & Figure 5), yet this did not result in the maintenance of the effective pedal force timing since it was shifted progressively later in the pedal cycle by approximately 30 degrees (Figure 7). The altered mechanical contribution of these muscles may be attributed to an activation-deactivation limitation since their duty cycles reached approximately 55% at 180 r.p.m. (Figure 6) such that they were active for more than half of the pedal cycle, inevitably contributing to negative muscular work. Similarly, most muscles displayed unique systematic phase shifts of muscle excitation relative to the pedal cycle (Figure 5) that were cadence and workload dependent explaining differences previously found for the timing of EMG for different muscles, cadences and workloads (Jorge and Hull, 1986; Sarre and Lepers, 2007). Differences in phase shifts between muscles that share similar functions, such as ST and BF (Figure 5), highlights the complexity of muscle control for this movement task.
The time-frequency properties of the EMG intensity during the bursts of muscle excitation were classified by their principal components, and general patterns of the PCfreq weights were seen for the first three principal components across all the muscles (Figure 2). PCfreq2 and PCfreq3 account for the time-varying intensity spectra as each burst of muscle excitation progresses, and the vectors describing their loading scores showed characteristic directions that changed at the cadence of maximum efficiency (Figure 2). Thus the efficiency of limb movement was related to the time varying frequency spectra of the EMG intensities. The frequency components of the EMG intensity spectra can be related to the type of motor units recruited (von Tscharner, 2000; Wakeling, 2009; Wakeling and Horn, 2009; Wakeling and Rozitis, 2004), although this has been controversial (Farina, 2008; von Tscharner and Nigg, 2008). The shifts in EMG frequency may result from the activation-deactivation limitations at the highest cadences, mentioned previously (Figure 6) and may reflect a shift in muscle fibre recruitment such that these muscles are still able to contribute to power production, while attempting to minimize negative muscular work (Figure 7: Sarre and Lepers, 2007).

This study investigated the influence of mechanical demands on muscle coordination during human limb movement, and the subsequent relationship between muscle coordination and movement performance parameters, mechanical efficiency and power output. Mechanical efficiency was maximized at increasing cadences for increasing power outputs, which corresponded to muscle coordination and altered the muscle fibre type recruitment that minimized the total muscle excitation across all muscles. In addition, mechanical power output was limited beyond a critical cycle frequency of 120-140 r.p.m., which was related to a breakdown in muscle coordination. The breakdown in muscle coordination was demonstrated by limits to minimum muscle burst duration, longer duty cycles and disproportionate
increases in muscle excitation for most muscles, suggesting a limitation of the activation-deactivation capabilities of the muscles, resulting in increasing metabolic costs and rapidly decreasing mechanical efficiency.
Author Contributions

OMB and JMW participated in the conception and design of the study as well as the data collection, analysis and interpretation. OMB was the primary author of the manuscript and JMW revised it. Both authors read and approved the final manuscript.

Funding

The study was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to JMW. OMB was supported by an NSERC Vanier Scholarship.
References


Figure Legends

Figure 1. The relations between total EMG intensity, power output and efficiency. (A) Efficiency at each power output where each point represents a pedal cycle. (B) Relationship between efficiency and total EMG intensity across all ten muscles where (C) shows mean values for each cadence-power output combination. Power outputs are represented by symbols (circle, 100 W; star, 200 W; square, 300 W and cross, 400 W) and cadences are represented by each color labeled (40 to 180 r.p.m.). Lines have been added to give a visual representation of the relationships across power outputs for each cadence and are solid grey (100 to 180 r.p.m.) and dashed black (40 to 80 r.p.m.) to better identify the different trends. Relationships across cadences at each power output are shown for mean +/- S.E.M. efficiency (D), and total EMG intensity across all muscles (E), and mean ineffective pedal force per pedal cycle (F). Lines are best-fit polynomials and squares show the maximum (D) or minima (E and F) for these curves. The dashed line in (E) shows the best-fit polynomial at 100 W for 40 to 120 r.p.m. with its minimum shown by the square marker: this reduced range of cadences matches that used by MacIntosh and co-workers (2000). Power outputs are identified as light grey through black for 100 through 400 W, respectively.

Figure 2. Principal component representation of the fluctuations in EMG intensity through time-frequency space for the bursts of muscle excitation and muscle specific total EMG intensities. Principal component representations of the time-varying frequency (PC_freq) of the muscle burst (contour plots; PC_freq1 top left, PC_freq2 top right and PC_freq3 bottom right for each muscle). Vectors represent the relationship between PC_freq2 (vertical)
and PCfreq3 (horizontal) loading scores at each cadence-power output condition and squares show cadences for maximum efficiency at each power output as determined in Figure 1. Line plots show mean +/- S.E.M. EMG intensity for each muscle at each cadence-power output condition, and are shown with the same grey scale as in Figure 1.

**Figure 3. Muscle coordination patterns for each cadence-power output combination.**

Mean EMG intensity pattern for each cadence (rows) and power output (columns) combination normalized to the maximum for each condition.

**Figure 4. Principal component representation of the muscle coordination.** Visual representations of the first five muscle coordination principal components (PC\textsubscript{mus}) and the relationship between mean PC\textsubscript{mus} loading scores (vertical axis) and efficiency (horizontal axis) for each cadence-power output condition. Power outputs are represented by symbols (circle, 100 W; star, 200 W; square, 300 W and cross, 400 W) and cadences are represented by each color labeled (40 to 180 r.p.m.) in PC\textsubscript{mus}1. Lines have been added to give a visual representation of the relationships across power outputs for each cadence and are solid grey (100 to 180 r.p.m.) and dashed black (40 to 80 r.p.m.) to better identify the different trends.

**Figure 5. Relative phase shifts of the total EMG intensity within the pedal cycle.** Phase shifts are shown across cadence values at each power output (first column) and across power outputs at each cadence (second column). Cadences listed in each plot in the second column indicate a significant effect of power output on the phase shift for that cadence. Power outputs in the first column are identified with the same grey scale as in Figure 1 as light grey through black for 100 through 400 W, respectively. Cadences are distinguished by dashing, as shown in Figure 7.
Figure 6. Muscle burst durations and duty cycles. Mean +/- S.E.M. muscle burst durations (first column) and duty cycle (second column) across cadences for each power output. The duty cycle represents the muscle burst duration as a percentage of the complete pedal cycle. Power outputs are identified with the same grey scale as in Figure 1 as light grey through black for 100 through 400 W, respectively.

Figure 7. Pedal forces. (A) Mean resultant (first column), effective (second column) and ineffective (third column) pedal forces for each power output and cadence. (B) Mean +/- S.E.M. pedal force per pedal cycle at each cadence. Best-fit polynomials have been fit to each power output with minima shown by square symbols. (C) Phase shift of each pedal force across cadences for each power output. Power outputs in (B & C) are identified with the same grey scale as in Figure 1 as light grey through black for 100 through 400 W, respectively. Cadences in (A) are identified in the second row.
<table>
<thead>
<tr>
<th>Cadence</th>
<th>100 W</th>
<th>200 W</th>
<th>300 W</th>
<th>400 W</th>
</tr>
</thead>
<tbody>
<tr>
<td>40 rpm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>60 rpm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>80 rpm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>100 rpm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>120 rpm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>140 rpm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>160 rpm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>180 rpm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Pedal Cycle (Degrees) | Scale
0 | 0.5 | 1