The Effect of Cadence on the Mechanics and Energetics of Constant Power Cycling

Running title: Effect of cadence on mechanics and energetics

Scott F. Brennan[1,2], Andrew G. Cresswell[1], Dominic J. Farris[1,3], and Glen A. Lichtwark[1]

[1]The University of Queensland, School of Human Movement & Nutrition Sciences, Centre for Sensorimotor Performance, Brisbane, Australia; [2]Liverpool John Moores University, Sport and Exercise Sciences, Liverpool, United Kingdom; [3]University of Exeter, Sport and Health Sciences, Exeter, United Kingdom

Corresponding author:
Scott F. Brennan
Liverpool John Moores University
Sport and Exercise Sciences
Tom Reilly Building, Byrom Street, Liverpool, L3 3AF
United Kingdom
email: S.Brennan@ljmu.ac.uk
phone: (+44) 151 904 8094

SF Brennan was supported by an Australian Postgraduate Award scholarship during the completion of this project. This project did not receive any external funding but did receive internal funding for the purchase of equipment. **Conflict of Interest:** The authors have no conflicts of interest to declare with professionals, companies or manufacturers who may benefit from the results of the present study. The results of the present study do not constitute endorsement by ACSM. The results of the study are presented clearly, honestly, and without inappropriate data manipulation.

Abstract

At a constant power output, cyclists prefer to use a higher cadence than those that minimise metabolic cost. The neuromuscular mechanism underpinning the preferred higher cadence remains unclear. **Purpose**. The aim of this study was to investigate the effect of cadence on joint level work and vastus lateralis (VL) fascicle mechanics while cycling at a constant, submaximal, power output. We hypothesised that preferred cycling cadence would enhance the power capacity of the VL muscle when compared to a more economical cadence. Furthermore, we predicted that the most economical cadence would coincide with minimal total electromyographic activity from the leg muscles. **Methods**. Metabolic cost, lower limb kinematics, joint level work, VL fascicle mechanics, and muscle activation of the VL, rectus femoris, biceps femoris, gastrocnemius medialis and soleus muscles were measured during cycling at a constant power output of 2.5 W/kg and cadences of 40, 60, 80 and 100 revolutions per minute (RPM). A preferred condition was also performed where cadence feedback was hidden from the participant. **Results**. Metabolic cost was lowest at 60 RPM, but the mean preferred cadence was 81 RPM. The distribution of joint work remained constant across cadences, with the majority of positive work being performed at the knee. The preferred cadence coincided with the highest VL power capacity, without a significant penalty to efficiency, based on fascicle shortening velocity. **Conclusions**. Cycling at a higher cadence is preferred to ensure that the muscle’s ability to produce positive power remains high. Further investigations are required to examine what feedback mechanism could be responsible for the optimisation of this motor pattern.

Keywords: vastus lateralis, work, power, efficiency, ultrasound, electromyography

Introduction

Humans are generally good at reducing metabolic cost for rhythmic movements, such as walking and running, by selecting a movement pattern that minimises energy expenditure at the required speed (1). However, both trained and untrained cyclists prefer to use cadences higher than those that minimise energy expenditure (2), suggesting that other factors influence the selection of the preferred cycling cadence.

Cycling provides a convenient movement pattern to examine the relationship between preferred movement, metabolic cost and muscle-tendon mechanics. The body's centre of mass moves very little relative to the bicycle in seated cycling, while the lower limb muscles perform work to overcome rolling and air resistance. In contrast to walking or running on a level surface, which requires negligible net work per cycle, cycling at a constant power output requires net positive work to be performed against the resistance provided at the cranks; the majority of which is performed by the knee and hip extensors (3,4). It is also possible to manipulate both resistance and cadence to maintain the same overall power output. For example, cycling with a low cadence and high pedal forces may produce the same power output as cycling with high cadence and low pedal forces. In both conditions, the joint ranges of motion remain relatively similar and only the velocity of movement varies. What is unclear is how the force and velocity requirements of the hip, knee and ankle muscles change with factors such as cadence, and how this might influence the preferred and/or most economical movement pattern.

Generally, the central nervous system is able to achieve the same overall mechanical output using many different motor strategies. Different strategies during cycling could change the distribution of power between joints, which would likely impact the metabolic cost of performing the movement because it relates to lower limb muscle performance (5). The sum of the lower limb average joint moments has been shown to decrease at higher cadences (6), indicating a reduced workload for the associated muscles. Forward dynamics simulations of cycling have shown an optimal cadence of 90 RPM at a relatively high power output (~3.5 W/kg). At this optimal cadence, which is similar to the preferred cadence for the power output assessed, neuromuscular parameters (e.g. muscle force, activation, stress) were minimised compared to lower or higher cadences (7). Combined with a close association between the most economical cadence and total average muscle activation (8), these results would suggest that the preference for cadences above the most economical may be related to muscle mechanical requirements and their activation conditions, rather than energetic cost.

Skeletal muscle has a limited capacity for force production that depends on the length and shortening velocities of the fibres. The fibres of each muscle have an optimum length for force production and will experience a hyperbolic decrease in force capacity as shortening velocity increases (9,10). The amplitude and velocity of muscle fibre shortening are therefore critical to a muscle's capacity to produce force and power during movements like cycling (11). These factors are also critical for determining the power output and efficiency of a muscle (12,13). Depending on the activation conditions, peak muscle power may be observed at faster shortening velocities than peak efficiency (12,13). As such, it may not be possible to maximise power and efficiency at the same cadence, which may impact on a cyclist's preferred cadence during cycling.

There were two main aims of this study: (1) to determine the effects of cadence on metabolic cost, joint level mechanical work, and cumulative muscle activation while cycling at a constant submaximal power output; (2) to determine the effect of cadence on vastus lateralis (VL) muscle fascicle mechanics and assess the implications for muscle power and efficiency. The fascicle mechanics of VL would be used as a representative muscle for the contractile mechanics of the quadriceps muscles. We hypothesised that the preferred cadence would be higher than the cadence that minimises metabolic cost and overall muscle activation, as has been reported previously (2), but that there would be no significant change in the distribution of joint work between the hip, knee and ankle with changes in cadence, because of the constraints of the pedal trajectory. On the basis that favourable muscle contractile dynamics is linked to overall metabolic economy, we hypothesised that the most economical cadence would coincide with VL shortening velocities that are most favourable for efficiency, which would minimise cumulative muscle activation of the VL. Since higher cadences should require higher muscle shortening velocities, we also hypothesised that the preferred cadence would require VL shortening velocities that are more favourable for VL power production.

Methods

Participants for this study were recruited from the staff and students of The University of Queensland. Ethical approval was granted from the institutional ethics committee. Written informed consent was obtained from the participants before commencing the experiment. Participants included 14 healthy adults (11 male, 3 female) that were capable but not competitive cyclists. The mean (± SD) age, height, and mass of all participants was 28 ± 5 years, 178 ± 6 cm, and 76 ± 9 kg, respectively.

This study utilised some muscle level data previously presented in Brennan et al. (2018), however additional data was also collected and analysed to achieve the unique aims of the current study (11).

Muscle force-length-velocity relationship

The method for determining the relationship between quadriceps force and VL fascicle length (isometric contractions) and velocity (isokinetic contractions) has been outlined in detail in Brennan et al. (2018); it is briefly detailed below (11).

After a familiarisation session (1-2 days prior to the experimental data collection) participants were seated in a dynamometer (HUMAC NORM, CSMi Inc., Stoughton, MA, USA) with a trunk angle of 80^0 (10^0 from upright) and adjusted to align the axle of the motor with the rotation axis of the left knee. After a standardised warm-up, participants performed three maximal effort, isometric contractions from 50^0 to 100^0 of knee flexion in 10^0 increments, in a randomised order (0^0 = full knee extension). A 120 s period of rest was given between trials to avoid potential fatigue effects. Participants then performed three, maximal effort, isokinetic knee extensions from 100^0 flexion to full extension at angular velocities of 50^0/s, 100^0/s, 200^0/s, 300^0/s, and 400^0/s, in a randomised order. A movement initiation threshold was set at 90% of the maximum isometric torque recorded at the 100^0 knee angle.

Knee extensor torque and joint angle were recorded at 2 kHz during each contraction (CED Micro 1401 A/D converter and Spike 2 software, Cambridge Electronic Design Ltd., Cambridge, England). The measured torque was corrected to account for the effect of gravity at different joint angles. To remove any inertial effects on the measured torque during acceleration of the dynamometer attachment, the mean torque and fascicle shortening velocity were measured during only the true isokinetic (constant angular velocity) portion of the movement.

Ultrasound images of VL muscle fascicles as well as its deep and superficial aponeuroses were simultaneously recorded with B-mode ultrasound using two flat ultrasound transducers (LogicScan 128, LV7.5/60/96Z transducers, 5 MHz central frequency, image depth of 50 mm and sample rate of 80 Hz, TELEMED, Vilnius, Lithuania) that were held end-to-end in a custom frame and secured to the lateral thigh (14). Markings were made on the skin with a semi-permanent marker so the position of the transducers could be replicated for the cycling protocol. Fascicle length changes during contractions were measured offline using a custom Matlab script (MathWorks Inc., Natick, USA) that used a semi-automatic tracking algorithm (15,16). Manual corrections of the fascicle end points were made if the tracking algorithm could not adequately detect fascicle length change from one frame to the next (assessed by the operator).

Quadriceps force was calculated as knee extensor joint torque divided by the angle specific moment arm, which was measured from a scaled musculoskeletal model created for each participant from the cycling data collection (17). Subject-specific force-length and force-velocity curves were produced using physiologically appropriate models as described thoroughly in Brennan et al. (2018) (11). Briefly, at each joint angle the maximum quadriceps force and corresponding fascicle length during isometric contraction was determined, based on two trials, and the relationship between force and fascicle length was fit (least square) with a parabolic function (18) for each participant. During the isokinetic contractions, the mean quadriceps force and corresponding fascicle shortening velocity was determined during the true isokinetic portion of the trial, to avoid any inertial effects. The maximum mean force produced from two trials at each velocity was used in a least square fit of a force-velocity relationship (19) for each participant. The goodness of fit was calculated separately for each participant.

Muscle power-efficiency relationship

Fascicle power-velocity and efficiency-velocity curves were generated for each individual. The power curve was generated as the product of force and velocity, based on the curve fit to the experimental data. The relationship between shortening velocity and muscle efficiency was generated using a model described by Lichtwark & Wilson (20). In this model, efficiency was defined as the muscle work produced divided by the energetic cost of performing that work (Efficiency = Work / [Heat + Work]). Work was defined as the time integral of the force multiplied by the velocity. Heat is the combination of heat generated to maintain an isometric force plus the heat of shortening. The rate of heat production was estimated from V_{max} and curvature of the force-velocity relationship (G) taken from the individual force-length and force-velocity curves. Assuming a maximum crossbridge activation rate, the maintenance heat rate was calculated as 8 (V_{max}/G^2) and shortening heat as V_{CE}/G (where V_{CE} is the instantaneous velocity of the contractile element). The efficiency was therefore equal to work divided by the sum of the maintenance heat, shortening heat, and work at each point on the velocity curve.

Cycling joint and muscle function

Protocol

The cycling protocol consisted of two sessions. In the first session, steady state oxygen consumption was measured (see *Metabolic Cost* below) during seated cycling on an ergometer (Lode Excaliber Sport, Lode B.V., Groningen, Netherlands) at a constant power output of 2.5 W/kg body mass, at predetermined cadences of 40 revolutions per minute (RPM), 60 RPM, 80 RPM and 100 RPM. A preferred condition was also completed, where cadence feedback was hidden and participants were instructed to cycle at the cadence that felt the “most comfortable”. The order of conditions was randomised. Shimano SPD-SL pedals and R078 cycling shoes were used for all conditions (Shimano Inc., Osaka, Japan). Seat height was normalised to 100% trochanter length (21), measured as the vertical distance from the greater trochanter to the base of the foot when standing. In the second session, surface electromyography (EMG) of leg muscles [VL, rectus femoris (RF), biceps femoris (BF), medial gastrocnemius (MG), and soleus (SOL)], three-dimensional (3D) kinematics of the lower limb, pedal force measurement using instrumented cranks (Swift Performance, Brisbane, Australia), and VL muscle fascicle length changes using B-mode ultrasonography were recorded while completing the same protocol and order of conditions. Data capture was synchronised using a logic pulse generated by the ultrasound to trigger data collection of the motion capture and EMG systems. Participants cycled at the target cadence for a minimum of 120 s and they could maintain a constant cadence (± 5 RPM). Data were recorded for a minimum of five pedal revolutions. The absolute time of the five revolutions varied across cadence conditions. Between conditions, participants cycled at 50 W at a self-selected cadence for 120 s of active rest.

Metabolic cost

Metabolic data was collected using open circuit spirometry (Vacumed Vista-MX2, Vacumetrics Inc., Ventura, California, USA). $\dot{V}O_2$ and $\dot{V}CO_2$ were measured continuously during exercise. The gas analysers were calibrated immediately prior to testing and validated between each condition using certified calibration gases to remove drift. The turbine calibration was checked prior to testing using a 3 L syringe. Resting $\dot{V}O_2$ was measured while seated on the bike for 3 to 5 minutes prior to the cycling protocol. Participants performed a brief warm up for 3 minutes at 100 W at a self-selected cadence while the experimental protocol was explained to them in detail. Participants cycled at the prescribed cadence for a minimum of 5 minutes to achieve steady state, with an equivalent rest period between conditions. Steady state was determined by a $< 10\%$ difference in $\dot{V}O_2$ over the final minute. Submaximal oxygen uptake was calculated from the mean $\dot{V}O_2$ of the final minute of data when steady state was achieved. Net metabolic power was calculated from equations based on O_2 consumption and CO_2 production (22).

Joint kinematics and kinetics

A six-camera optoelectronic motion analysis system (Qualisys, Gothenburg, Sweden) was used to capture the locations of 23 passive, reflective markers positioned on anatomical landmarks on the pelvis, left thigh, left shank and left foot at a sample rate of 200 Hz. Scaling markers were placed on the anterior and posterior iliac spines, greater trochanter, medial and lateral epicondyles, medial and lateral malleoli, calcaneus, 1st and 5th metatarsal heads. A static calibration capture was collected while standing upright with arms crossed to opposite shoulder. A custom Matlab script was used to scale the model size and segmental inertial parameters in OpenSim software v3.3 on a modified version of the OpenSim *gait 2392* model (23). Additional clusters of dynamic tracking markers mounted on semi-rigid plates were placed on the lateral mid-thigh, and mid-shank for movement trials. Kinematic data was exported for analysis using Matlab and OpenSim. Radial and tangential crank forces as well as crank position were measured from the instrumented cranks (Swift Performance, Brisbane, Australia). The forces were transformed from the crank frame of reference to the global coordinate system using standard rotation matrices and the crank angle. The resultant pedal reaction force was applied to the foot segment of the rigid body model, using an inverse dynamics approach to calculate joint moments. Joint mechanical power was calculated as the product of the calculated joint moment and angular velocity. Joint mechanical work per revolution was calculated as the time integral of mechanical power per cycle.

Fascicle length

Ultrasound images were simultaneously recorded from the VL muscle using the same method as described earlier. The same two ultrasound transducers were secured to the lateral thigh in the same location as the dynamometer protocol and the same method for tracking was used. The same cycles that were analysed for the kinematics/kinetics were analysed to determine change in fascicle length as a function of crank angle. If a cycle could not be tracked, the next consecutive cycle was used.

Muscle activation

Surface EMG was collected from the VL, RF, BF, MG, and SOL muscles using a wireless EMG system (Myon 320 system, Myon AG. Baar, Switzerland). Placement of the electrodes was based on SENIAM guidelines with an inter-electrode distance of 2 cm (24). Electrode sites were shaved, and cleaned using an abrasive gel (Nuprep Skin Prep Gel, Weaver and Company, Aurora, Colorado, USA) and rubbing alcohol. EMG signals were recorded at 2 kHz. All EMG signals were digitally band-pass filtered between 15-500 Hz to remove non-physiological signals and offset removed by subtracting the median activation from the signal for each muscle. The filtered signals were then processed by calculating the root mean square (RMS) over a moving window width of 50 ms. EMG signals for each muscle were normalized to the mean of the maximal activation per cycle during the preferred cadence condition. To quantify the amount of muscle activation per cycle, the EMG signal for each muscle was integrated with respect to time. Cumulative muscle activation was calculated by multiplying the integrated muscle activation per cycle by the cadence (RPM) to calculate the cumulative activation per minute. To scale the activation of each muscle to a physiologically appropriate value before summing to attain total muscle activation, each muscle's cumulative activation was multiplied by its relative mass (25).

Analysis

VL fascicle lengths and velocities recorded during the cycling task were normalised to optimal length (from the individual force-length curve) and maximal shortening velocity (from the individual force-velocity curve), respectively. To determine the effect of cadence on the power and efficiency of VL, average power and efficiency was calculated from the individual power and efficiency curves for each cadence. For each cadence condition and each individual participant, the average power and efficiency during the concentric action of VL were calculated based on the average normalised velocity during the period when there was a positive knee extension moment and concomitant fascicle shortening. From here on, power or efficiency capacity refers to the average value calculated for each condition.

Statistical comparisons were performed using Graphpad Prism 7 (GraphPad Software Inc., La Jolla, CA, USA). A repeated measures ANOVA was performed across cadence conditions and Holm-Sidak multiple comparisons tests were used to compare each of the fixed cadences with the preferred cadence condition. Alpha was set at 0.05 for all tests. All waveform data is presented as an average of the crank revolution (top-dead-centre = 0^0).

Results

Of the 14 participants to complete all of the testing sessions, some data had to be removed due to technical issues, or insufficient ultrasound images to reliably track VL fascicles in all conditions. As a result, 12 data sets were analysed for the metabolic data, 11 for the kinematics and kinetics, 10 for muscle fascicle tracking, and 11 for the muscle activation data. In relation to the above, the metabolic energy data (and consequently all cycling data) was excluded if the participant did not reach steady state for all conditions, the kinematic and kinetic data was excluded if the instrumented cranks did not transmit crank force data for all conditions, muscle fascicle data was excluded if it could not be reliably tracked for both the dynamometer and cycling data, and muscle activation data was excluded due to movement artefact or transmitter issues. The mean ± SD for age, height and mass of the participants that determined the final results were 28 ± 5 years, 177 ± 6 cm, and 73 ± 7 kg, respectively.

Metabolic cost

The mass-relative power output of the protocol required an average power output of 183 ± 17 W. There was a significant main effect of cadence on net metabolic power ($p < 0.01$, $n = 12$) with the minimal metabolic costs occurring at 60 RPM (Figure 1). The preferred cadence was 81 ± 12 RPM.

The post-hoc analysis showed significantly lower metabolic cost at 60 RPM and significantly greater metabolic cost at 100 RPM compared to the preferred cadence.

Kinematics & Kinetics

The inverse dynamics analysis (n = 11) showed that the knee extensors produced a large joint moment during the first half (down-stroke) of the pedal revolution (Figure 2a). There was a systematic decrease in peak hip extension, knee extension and ankle plantar flexion moments with increasing cadence ($p < 0.01$). The plantar flexion ankle moments were considerably lower (30-50%) than the hip and knee joint moments. Predictably, due to the increased crank angular velocity, there was a systematic increase in joint angular velocities with increasing cadence (Figure 2b). There was not a significant difference in peak knee positive powers across conditions (Figure 2c).

Predictably, we observed significantly greater positive work per cycle at slower cadences for all joints, however the distribution of joint positive work between the hip, knee, and ankle remained similar across cadences (Figure 3). For the knee joint, positive work was significantly greater for the 40 and 60 RPM conditions and significantly smaller for the 100 RPM condition compared to the preferred cadence. Collectively, total limb positive work per revolution significantly decreased with increasing cadence, whereas total limb negative work was not affected by cadence.

Muscle mechanics

The group mean (± SD) R^2 value for the curve fits of the individual force-velocity curves was 0.78 ± 0.17 (11). The isokinetic experiments yielded estimates of peak VL fascicle power at approximately 25% of V_{max} (1.2 L_0/s), of which only the 80 and 100 RPM conditions reached the necessary shortening speed for peak power (Figure 4a). Peak VL fascicle efficiency was estimated to occur at 19% of V_{max} (0.96 L_0/s), which was closer to the peak shortening velocities of the 40 RPM condition. There was a significant main effect of cadence on the power capacity during the period of positive power generation ($p < 0.01$). The mean power capacity increased to a maximum at 80 RPM with significantly lower average power capacity at 40 RPM (Figure 4b). Cadence also had a significant main effect on the mean efficiency capacity, ranging from 0.19 ± 0.06 at 40 RPM to 0.21 ± 0.05 at 80 RPM.

Activation

The effect of cadence on peak muscle activation was variable across muscles. There were no significant effects of cadence on the peak activation of VL, RF, SOL, or BF; while MG did show a significant increase in peak activation as cadence increased ($p < 0.01$). Thus, there was not a consistent pattern across all muscles or muscles within the same group for peak EMG to increase or decrease with cadence. When accounting for the different duration and number of revolutions for each cadence condition, there was a statistically significant increase in cumulative activation for all muscles (Figure 5a,b, $p < 0.01$). When combined, there was also a significant effect of cadence on the total cumulative muscle activation of all muscles ($p < 0.01$). The total cumulative muscle activation for all muscles showed a similar pattern to net metabolic power (Figure 5c) with lower overall activation at slower cadences.

Discussion

This study examined the effect of cycling cadence on VL fascicle mechanics, joint mechanical work, muscle activation, and whole-body metabolic cost during seated cycling. The data presented provides a unique insight into determining how muscle fascicle mechanics relates to muscle energetics during cycling. Our data demonstrates that cadence did not alter the ratio of work production across different joints. Contrary to our hypothesis, VL efficiency (based on VL fascicle shortening velocity) was favourable for both the most economical cadence and preferred cadence. However, the preferred cadence had shortening velocities that were most favourable for the power generating capacity of VL. The total muscle activation per unit time was reduced at the most economical cadence which is consistent with the findings of Marsh and Martin (1995) (8). This work demonstrates the mechanisms that allow humans to be more economical at a cycling cadence that is lower than they would naturally prefer to pedal. The results also suggest that the preferred cadence is more favourable for the muscle power capacity of major work producing muscles, such as VL.

Joint work contributions to cycling energetics

Cycling at different cadences at a constant submaximal power output resulted in consistent changes in joint work requirements and joint velocity across conditions. Forward dynamic simulations show the distribution of work between the hip, knee and ankle is a mechanical requirement to produce the energy to accelerate the crank (26,27). The uniarticular hip (gluteus maximus) and knee extensors (VL) generate the majority of the work to accelerate the crank, while the ankle plantar flexors (MG and SOL) transfer energy from the proximal muscles to the crank. Since the joint angular velocities are constrained by the crank velocity, there is a consistent distribution of joint work across cadence conditions (28). In this data, the knee and hip were the major contributors of positive work, as would be expected for seated cycling at submaximal intensities (29), with the knee performing approximately 70% of the total joint work per cycle. Importantly, there was no significant change in the distribution of positive work between the joints across cadence: the participants increased the total work as required but did not shift the proportions of work from one joint to another. An alternative strategy could have been to shift a portion of the total work from the knee to the hip or ankle as cadence changed. It appears that the pedalling strategy is constrained by the requirement to produce energy to accelerate the crank (26,27). While the total amount of work performed by each joint in a single revolution decreases with increased cadence, the total net work performed over time should remain similar. Therefore, changes in joint work contributions are unlikely to contribute to changes in metabolic cost at different cadences.

Knee joint kinetics, fascicle dynamics and the relationship to muscle activation and cycling energetics

The changes in joint moments and mechanical work across cadence conditions indicate changes in muscle force and work production across cadence conditions. The greater knee joint moments and positive work at slow cadences must be produced by the quadriceps muscles, of which VL constitutes approximately 40% of the total physiological cross sectional area (25), and requires shortening of the muscle as the knee extends during the downstroke. We have previously shown, using this same data, that fascicle shortening and shortening velocity is significantly impacted by cadence and that there is a non-linear change in the VL fascicle shortening velocity with increased cadence, due to the involvement of the series elastic structure in absorbing and generating energy (11).

Here we have estimated the effect that the different VL fascicle velocities would have on muscle power and efficiency. Based on data collected using isokinetic contractions and a model of energetics, we estimated peak efficiency to be 19% of maximum shortening velocity (V_{max}) compared to peak power at 25% V_{max}. The average fascicle shortening velocity resulted in the highest average VL power capacity occurring at 80 RPM, while the power capacity was significantly reduced at 40 RPM. The peak instantaneous fascicle shortening velocities when cycling at the slowest cadence (40 RPM) did not reach the peak of the power curve, occurring entirely on the ascending section. Therefore, pedalling at slower cadences results in VL fascicle shortening velocities that are less suitable for the power capacity of the muscle. However, the velocities of shortening at the preferred and most economical cadences resulted in similar overall VL efficiency estimates. As such, changes in VL fascicle velocity across a cycle are unlikely to explain the decreased metabolic cost at 60 RPM versus preferred.

The nervous system must activate muscles based on the force requirements of the movement and the functional capacity of the muscle to produce those forces. This ultimately affects metabolic cost, as muscles must activate/deactivate with varying magnitudes, rates, and durations. We did not observe consistent changes in EMG amplitude for all muscles across cadence conditions, which is most likely due to the concurrent changes in the force and velocity requirements of each muscle. For example, peak VL activation was not significantly affected by cadence, but the required forces are greater and fascicle shortening velocities lower at slow cadences compared to fast cadences. Thus, the VL force produced relative to the peak activation is greater at slow cadences compared to fast cadences, which coupled with the higher economy of low frequency contractions (30) may reduce the activation costs of force production at lower cadences (60 RPM). It is also possible that higher frequency contractions at higher cadence require faster motor units to achieve the required activation/deactivation rate (31,32), which might also incur a greater cost.

Muscle activation and the most economical cadence

The metabolic curve generated from the muscle activation data showed a curvilinear relationship, similar to that of previous data of comparable power outputs (33). There was a significantly greater metabolic cost to cycling at the preferred cadence (81 ± 12 RPM) compared to the most economical cadence of 60 RPM. Individual muscles exhibited different relationships between cadence and cumulative activation, making it difficult to identify specific muscles that might dominate changes in cumulative activation costs. Blake and Wakeling (2015) explored the effect of cadence and power output on efficiency (ratio of pedal power to total EMG intensity) and coordination, showing that the most efficient cadence (60 RPM at 100 W, 77 RPM at 200 W) is related to minimising total muscle excitation. Uniarticular muscles like VL and SOL showed consistent EMG intensity until the highest cadences (>120 RPM), whereas biarticular muscles like RF and MG exhibit greater changes in EMG intensity across lower cadences (40-120 RPM) (34). Our results differed in that both uni-articular (e.g. VL, SOL) and bi-articular muscles (e.g. RF, MG) in this study showed an increase in cumulative activation with cadence. This is most likely the result of representing EMG intensity per cycle compared to EMG per unit time, such that high cadences require a greater number of activation/deactivation cycles for a given distance/time. Our results primarily show that total cumulative activation is greater above the most economical cadence. Not only is there an increased number of activations for a given time period, but high frequency, short duration contractions have been shown to be less economical (30). Despite the increased force requirements, it appears to be beneficial in terms of activation cost and overall metabolic cost to cycle at slower cadences.

The relationship between muscle work and power, and the preferred cycling cadence

The preference for a particular cycling cadence, likely has a link to muscle contraction dynamics and the nervous system' knowledge of muscle performance parameters. Neptune and Hull (1999) argue, based on computer simulations, that the preferred cadence might minimise muscle force, stress and activation all major muscle groups are considered (7). Such simulations attempt to account for changes in muscle dynamics and how this influences their mechanical state and output, however the precise contractile conditions (e.g. fibre velocity and power output) were not explored in this study. Our results indicate that as cadence increased, there was an increase in VL fascicle shortening velocity and fascicle power capacity such that the mean power capacity was greatest at the preferred cadence and 80 RPM conditions. Thus, in cycling where there is a mechanical requirement for net positive power, a higher cadence than the most economic cadence is beneficial for producing VL muscle power. Therefore, it could be suggested that when the goal is to produce net positive power, a motor pattern that maximises the capacity for muscle power is utilised. At present, it is not clear how the nervous system would assess instantaneous muscle power relative to its maximal power capacity. Furthermore, a similar comment could be made regarding detection of metabolic rates relative to muscle mechanical energy for maximising movement efficiency.

One potential benefit of choosing a preferred cadence that favours muscle power is that it could provide a buffer against the steep ascending slope of the power and efficiency curves at low shortening velocities. If the shortening velocity of VL at the preferred cadence was concentrated at peak efficiency, and cadence was to decrease during the movement due to a sudden increase in power requirements (e.g. riding up a hill), the shortening velocity and subsequent power output from the muscle would reduce rapidly. Selecting a preferred cadence that results in shortening velocities near peak power means that variations in cadence (and shortening velocity) would have limited effects on power and efficiency.

While the power capacity of VL appears to be maximised at the preferred cadence (near 80 RPM) for power output used this study (2.5W/kg or ~ 180W), a question remains as to whether the VL power output remains optimal with increased external power output requirements (33). At submaximal power outputs, as used in this study, positive power is primarily contributed by knee extension (28). However, as the overall external power requirements increase, there are greater relative contributions from hip extension and knee flexion power (29). This may suggest that power output of the knee may be limited by the requirement to shorten at high velocities and that power increases are mainly driven primarily by the hip. However, we have previously also shown that as cadence increases for a given power output, the reduction in knee extension moment allows the VL fascicle average shortening velocity to remain relatively constant (11), even though the MTU shortens at progressively higher rates. This is a consequence of the reduced requirement to stretch the elastic tissues due to lower forces being transmitted at higher cadence. Therefore, increasing cadence at higher power outputs reduces the required force with potentially little effect on the net fascicle shortening velocity; allowing the fascicles to still operate at near optimum velocity for generating maximum power. This hypothesis requires further experimental testing to confirm.

Limitations

There are a large number of muscles that actuate the hip, knee, and ankle joints in cycling, of which we have elected to observe changes in the largest of the quadriceps muscles. It is possible that other muscles such as RF and BF are also significantly affected by cadence, however those muscles do not have the architecture that is suitable for the in vivo fascicle tracking method used in this study. As such, we elected to investigate a primary force producing muscle in cycling (VL) that allowed for measurement of in vivo fascicle mechanics. Furthermore, the position of the hip during the dynamometer task is not the same as the hip angle in cycling, since it is a dynamic multi-joint movement. The lengths of other muscles (RF, BF etc.) crossing the hip may therefore be affected by the chosen dynamometer hip angle.

We have used isokinetic maximum voluntary contractions to determine the relationship between force and velocity for VL. This has some potential limitations, particularly given that the highest achievable joint angular velocity was less than half that which would be required to achieve the true VL muscle-tendon unit V_{max} (35). However, we have achieved similar force-velocity curves and estimations of V_{max} to those already reported in the literature (35,36). The isokinetic data used to form the force-velocity curve in this study spans the range of shortening velocities at which peak power and efficiency was observed, as well as the cycling conditions. Therefore, the force-velocity curve has been measured up to the relevant shortening velocities to determine peak power and efficiency.

We have also based our estimates of efficiency off a model that assumes a linear relationship between shortening velocity and energy consumed by the muscle. The slope of this relationship may vary, which can influence the velocity that peak efficiency will occur. To inform the model we used parameters that match mammalian muscle (37) with properties intermediate to slow and fast twitch fibres. It is likely that higher cadences will require greater numbers of fast fibres, which may further increase the velocity at which maximal efficiency occurs (13), however this is only likely to increase the efficiency value of the highest cadence, perhaps making efficiency based on velocity relatively flat across the cadence range.

Conclusions

These results support previous evidence that cyclists do not automatically select the most economical cadence, and instead prefer to use a higher cadence that has significantly greater metabolic cost. The most economical cadence appears to be the result of lower total cumulative muscle activation, and favourable VL shortening velocities for muscle efficiency, although the preferred cadence also had velocities favourable for high efficiency. There was no change in the proportion of work done at each joint that could account for differences in metabolic rate across cadence conditions. When pedalling at the preferred cadence, we observed fascicle shortening velocities that were favourable for muscle power capacity as well as efficiency. These results not only inform the mechanics and energetics of cycling but provide useful insight to the neuromuscular mechanism that might influence preferred movement patterns, particularly in tasks that require net positive power.

Acknowledgments

SF Brennan was supported by an Australian Postgraduate Award scholarship during the completion of this project. This project did not receive any external funding but did receive internal funding for the purchase of equipment.

Conflict of Interest

The authors have no conflicts of interest to declare with professionals, companies or manufacturers who may benefit from the results of the present study. The results of the present study do not constitute endorsement by ACSM. The results of the study are presented clearly, honestly, and without inappropriate data manipulation.

References

1. Holt KG, Hamill J, Andres RO. Predicting the minimal energy costs of human walking. Med Sci Sports Exerc. 1991 Apr;23(4):491–8.
2. Marsh AP, Martin PE. Effect of cycling experience, aerobic power, and power output on preferred and most economical cycling cadences. Med Sci Sports Exerc. 1997 Sep;29(9):1225–32.
3. Ericson MO, Bratt A, Nisell R, Németh G, Ekholm J. Load moments about the hip and knee joints during ergometer cycling. Scand J Rehabil Med. 1986;18(4):165–72.
4. Ericson MO, Bratt Å, Nisell R, Arborelius UP, Ekholm J. Power output and work in different muscle groups during ergometer cycling. Eur J Appl Physiol. 1986 Jun;55(3):229–35.
5. Sawicki GS, Lewis CL, Ferris DP. It pays to have a spring in your step. Exerc Sport Sci Rev. 2009 Jul;37(3):130–8.
6. Marsh AP, Martin PE, Sanderson DJ. Is a joint moment-based cost function associated with preferred cycling cadence? J Biomech. 2000 Feb;33(2):173–80.
7. Neptune RR, Hull ML. A theoretical analysis of preferred pedaling rate selection in endurance cycling. J Biomech. 1999 Apr;32(4):409–15.
8. Marsh AP, Martin PE. The relationship between cadence and lower extremity EMG in cyclists and noncyclists. Med Sci Sports Exerc. 1995 Feb;27(2):217–25.
9. Gordon AM, Huxley AF, Julian FJ. The variation in isometric tension with sarcomere length in vertebrate muscle fibres. J Physiol-London. 1966 May;184(1):170–92.
10. Hill AV. The heat of shortening and the dynamic constants of muscle. P Roy Soc B-Biol Sci. 1938 Oct;126(843):136–95.

11. Brennan SF, Cresswell AG, Farris DJ, Lichtwark GA. The effect of muscle-tendon unit vs. fascicle analyses on vastus lateralis force-generating capacity during constant power output cycling with variable cadence. J Appl Physiol. 2018 Apr 1;124(4):993–1002.

12. Curtin N, Woledge R. Power at the expense of efficiency in contraction of white muscle fibres from dogfish *Scyliorhinus canicula*. J Exp Biol. 1996;199(3):593–601.

13. Barclay CJ. Efficiency of fast- and slow-twitch muscles of the mouse performing cyclic contractions. J Exp Biol. 1994 Aug;193:65–78.

14. Brennan SF, Cresswell AG, Farris DJ, Lichtwark GA. In vivo fascicle length measurements via B-mode ultrasound imaging with single vs dual transducer arrangements. J Biomech. 2017 Nov;64:240–4.

15. Cronin NJ, Carty CP, Barrett RS, Lichtwark G. Automatic tracking of medial gastrocnemius fascicle length during human locomotion. J Appl Physiol. 2011 Nov;111(5):1491–6.

16. Farris DJ, Lichtwark GA. UltraTrack: Software for semi-automated tracking of muscle fascicles in sequences of B-mode ultrasound images. Comput Methods Programs Biomed. 2016 May;128:111–8.

17. Delp SL, Anderson FC, Arnold AS, Loan P, Habib A, John CT, et al. OpenSim: open-source software to create and analyze dynamic simulations of movement. IEEE Trans Biomed Eng. 2007 Nov;54(11):1940–50.

18. Azizi E, Roberts TJ. Muscle performance during frog jumping: influence of elasticity on muscle operating lengths. Proc R Soc B. 2010 May 22;277(1687):1523–30.

19. Curtin NA, Woledge RC. Power output and force-velocity relationship of live fibres from white myotomal muscle of the dogfish, *Scyliorhinus Canicula*. J Exp Biol. 1988;140:187–97.

20. Lichtwark GA, Wilson AM. A modified Hill muscle model that predicts muscle power output and efficiency during sinusoidal length changes. J Exp Biol. 2005 Aug;208(15):2831–43.
21. Nordeen-Snyder KS. The effect of bicycle seat height variation upon oxygen consumption and lower limb kinematics. Med Sci Sports. 1976;9(2):113–7.
22. Brockway JM. Derivation of formulae used to calculate energy expenditure in man. Hum Nutr Clin Nutr. 1987 Nov;41(6):463–71.
23. Delp SL, Loan JP, Hoy MG, Zajac FE, Topp EL, Rosen JM. An interactive graphics-based model of the lower extremity to study orthopaedic surgical procedures. IEEE Trans Biomed Eng. 1990;37(8):757–67.
24. Hermens HJ, Freriks B, Disselhorst-Klug C, Rau G. Development of recommendations for SEMG sensors and sensor placement procedures. J Electromyogr Kinesiol. 2000 ed. 2000 Oct;10(5):361–74.
25. Ward SR, Eng CM, Smallwood LH, Lieber RL. Are current measurements of lower extremity muscle architecture accurate? Clin Orthop. 2009 Apr;467(4):1074–82.
26. Neptune RR, Herzog W. Adaptation of muscle coordination to altered task mechanics during steady-state cycling. J Biomech. 2000 Feb;33(2):165–72.
27. Raasch CC, Zajac FE. Locomotor strategy for pedaling: muscle groups and biomechanical functions. J Neurophysiol. 1999 Aug 1;82(2):515–25.
28. Ericson MO. Mechanical muscular power output and work during ergometer cycling at different work loads and speeds. Eur J Appl Physiol. 1988;57(4):382–7.
29. Elmer SJ, Barratt PR, Korff T, Martin JC. Joint-specific power production during submaximal and maximal cycling. Med Sci Sports Exerc. 2011 Oct;43(10):1940–7.

30. Hogan MC, Ingham E, Kurdak SS. Contraction duration affects metabolic energy cost and fatigue in skeletal muscle. Am J Physiol. 1998 Mar;274(3):E397–402.

31. Blake OM, Wakeling JM. Early deactivation of slower muscle fibres at high movement frequencies. J Exp Biol. 2014 Oct 1;217(Pt 19):3528–34.

32. Wakeling JM, Uehli K, Rozitis AI. Muscle fibre recruitment can respond to the mechanics of the muscle contraction. J R Soc Interface. 2006 Feb 10;3(9):533–44.

33. Coast JR, Welch HG. Linear increase in optimal pedal rate with increased power output in cycle ergometry. Eur J Appl Physiol. 1985 Feb;53(4):339–42.

34. Blake OM, Wakeling JM. Muscle coordination limits efficiency and power output of human limb movement under a wide range of mechanical demands. J Neurophysiol. 2015 Dec;114(6):3283–95.

35. Hauraix H, Dorel S, Rabita G, Guilhem G, Nordez A. Muscle fascicle shortening behaviour of vastus lateralis during a maximal force-velocity test. Eur J Appl Physiol. 2017 Feb;117(2):289–99.

36. Fontana H de B, Roesler H, Herzog W. In vivo vastus lateralis force-velocity relationship at the fascicle and muscle tendon unit level. J Electromyogr Kinesiol. 2014 Dec;24(6):934–40.

37. Barclay CJ, Constable JK, Gibbs CL. Energetics of fast- and slow-twitch muscles of the mouse. J Physiol-London. 1993 Dec;472:61–80.

Figure Legends

Figure 1. Net metabolic power as a function of cadence. There was a significant effect of cadence on metabolic cost, with the minimum occurring at 60 RPM. The preferred cadence of 81 RPM recorded a significantly higher metabolic cost than 60 RPM and a significantly lower cost compared to 100 RPM. Data points means ± standard deviation. Astricts (*) show significant differences versus the preferred cadence.

Figure 2. Group mean waveforms for knee joint kinematics and kinetics. There was a knee extension moment (a) during the first half of the cycle that decreased with increasing cadence. Joint velocity (b) increased with cadence due to a faster crank angular velocity. (c) The knee joint exhibited two periods of positive power: a large positive power period during the down stroke, which coincides with the knee extension moment and a lesser period as the knee joint flexed during the upstroke. Different line types represent the different cadences. The mean preferred cadence condition is not shown as it closely resembles the 80 RPM condition. Error bars show ± 1 standard deviation for the preferred cadence condition.

Figure 3. Group mean positive work per revolution for each of the lower limb joints for the 40, 60, 80, and 100 RPM conditions. The radius of each concentric circle is scaled to the summed positive work of all the joints and shows that as cadence increased, the amount of positive work per revolution decreased. The distribution of positive work across the three joints remained relatively constant. The knee provided the largest proportion of total limb work, followed by the hip and then ankle.

Figure 4. The effect of cadence on VL fascicle mechanics relative to the force-velocity relationship and estimated average power and efficiency. (a) As cycling cadence increased, peak VL shortening velocities were closer to the peak of the power curve (grey, dot-dash) compared to slower cadences that are closer to the peak of the efficiency curve (grey, dot). Vertical lines show the group mean peak shortening velocity for each cycling cadence. The curves shown are group means which demonstrate the shape of the relationship. (b) The power capacity was significantly different across cadence conditions with a peak at 80 RPM. The efficiency capacity (reported as a fraction of work output relative to predicted energetic cost) was significantly affected by cadence across conditions, with decreased efficiency at 40 RPM. Data are shown as mean ± standard deviation. Grey symbols show the preferred cadence.

Figure 5. Muscle activation of four lower limb muscles at each cadence. There was an increase in cumulative activation with cadence for the (a) quadriceps (VL, RF) and (b) plantar flexor (MG, SOL) muscles, which generally increased as cadence increased. (c) There was a curvilinear increase in the total cumulative activation with greater overall activation as cadence increased (left axis). Total activation represents the sum of the mass relative, cumulative muscle activations of the VL, RF, BF, MG and SOL muscles. Biceps femoris was omitted from for clarity. Error bars show the standard deviation.