Muscle coordination is key to the power output and mechanical efficiency of limb movements

J. M. Wakeling*, O. M. Blake and H. K. Chan

Department of Biomedical Physiology and Kinesiology, Simon Fraser University, Burnaby, BC, Canada, V5A 1S6

*Author for correspondence (wakeling@sfu.ca)

SUMMARY

The purpose of this study was to determine which features of muscle mechanics and muscle coordination affect the power output from a limb during locomotion. Eight subjects were tested while cycling at maximum exertion for 25 min on a stationary dynamometer. Cadence and load were varied to span a range of power outputs and myoelectric activity was measured from 10 muscles in the leg. Cycle-by-cycle variations in muscle coordination, cadence and power output were observed and the EMG intensity across all muscles was used as an estimate of the metabolic cost for each cycle. Data for the cycles at greatest power output were separated into three groups: maximum power, 80% power but lower EMG intensity and 80% power and higher EMG intensity. Torque–angular velocity relations were determined for the ankle and knee joints. During cycling at maximum power output the ankle joint was not extending at the velocity necessary for maximum power output; thus, maximum limb power occurs when some of the individual muscles cannot be generating maximum power output. Increases in EMG intensity occurred with no increase in power output from the limb: these corresponded to decreases in the efficiency and changes in coordination. Increases in power were achieved that were not matched by equivalent increases in EMG intensity, but did occur with changes in coordination. It is proposed that the power output from the limb is limited by the coordination pattern of the muscles rather than the maximum power output from any one muscle itself.

Key words: muscle, power, efficiency, limb, EMG, wavelet.

INTRODUCTION

Locomotion is an energetically expensive behaviour. Mechanical work is required for accelerating the body centre of mass and individual limb segments, for changing direction and for moving against a resistive force such as in cycling, swimming and animal flight. There is a metabolic cost to producing mechanical work from the muscles, and the ratio of the mechanical work to the total metabolic cost is the muscle efficiency (Woledge et al., 1985). Both the mechanical power production and the muscle efficiency depend on the rate at which the muscle shortens. The maximum power output from the muscles occurs while they are maximally active and shorten at their 'optimal speed'; that is, approximately 25–36% of their maximum intrinsic speed (Josephson, 1999; Kushermick and Davies, 1969; Swoap et al., 1997; He et al., 2000), whilst the maximum muscle efficiency has been reported at a similar range of 15–29% of their maximum intrinsic speed (Hill, 1964; He et al., 2000). Vigorous activity can result in the metabolic rate reaching 20 times the resting levels (Young et al., 1959) with most of this increase being due to skeletal muscle contractions. Minimizing the metabolic cost of high performance activities requires that the limbs generate large power outputs while the muscles perform work at high muscle efficiencies.

It is tempting to assume that when a limb is generating maximal power, each of its muscles is in turn operating at its maximal power output. However, such a situation may not be the most efficient, or even physiologically possible, and thus may not be the solution to the motor control task. Maximum muscle power output occurs when the muscle is fully activated and shortening at its optimal speed; however, muscles are rarely fully activated and anatomical constraints such as moment arm lengths, fibre pennation angles and tendon compliance may prevent the muscle from shortening at its optimal speed for a given motion (Lieber and Fridén, 2000). Furthermore, moment arms that change throughout the range of motion of a joint mean that the muscles may not necessarily shorten at their optimal speed even though a joint is rotating at its optimal angular velocity for maximal power output. Additionally, the action of multiple muscles about each joint means that not all muscles may be shortening at their optimal speed for a given angular velocity of a joint. Nonetheless, optimal angular velocities occur at the joints for the generation of maximal joint power for both isotonic movements (Tihanyi et al., 1982) and cyclic contractions (Sargeant et al., 1981; Zoladz et al., 2000) in a similar manner to the optimal speed for muscle contractions mentioned above.

Muscles may contribute to a range of functions during a movement: muscles spanning a single joint may be important for producing joint power, whereas multi-joint muscles are important for controlling the direction of the external force (van Ingen Schenau et al., 1992). Activity in a two-joint muscle may produce joint moments in a useful direction at one joint but in a paradoxically inappropriate direction in the other, and this has been called Lombard's paradox (Lombard, 1903). This paradoxical activity has the potential to decrease efficiency when compared with single-joint muscles (Gregor et al., 1985). However, co-contractions of antagonistic single and multi-joint muscles must occur in order to result in the correct power production combined with the correct force vector for the locomotor task, even though the co-contractions may reduce the net joint torque or power.

Muscle coordination refers to how the muscles work together and can be considered in terms of both the relative timing and relative magnitude of their contractions [for a review of EMG during cycling

see Hug and Dorel (Hug and Dorel, 2009)]. Previous studies have shown that differences in the relative magnitude of the muscle activities occur in response to varied crank torque and cadence (Wakeling and Horn, 2009) and the unusual effect of an elliptical front gear (Neptune and Herzog, 2000); additionally, the relative timing of muscle activities varies in response to changes in pedal cadence (Wakeling and Horn, 2009). Here it is proposed that the power output and efficiency of the limb motion are limited by the coordination patterns between the muscles, and not the maximum power achievable by the individual muscle groups *per se*. The purpose of this study was to quantify the fluctuations of power output and efficiency during an intensive locomotor task and to test whether limb power is associated with the absolute levels of muscle activity (a determinate of muscle power), or muscle coordination. Our second aim was to determine whether the joints rotate at the angular velocities needed for maximum power output when the limb generates maximum power.

MATERIALS AND METHODS
Subjects
Data were collected from eight male cyclists (age 36.9±3.7 years; mass 74.4±3.2 kg; height 1.80±0.03 m: means ± s.e.m.). All subjects gave their informed written consent to participate in the study, in accordance with Simon Fraser University Office of Research Ethics approval.

Cycle testing
Locomotor performance was tested during cycling on an indoor cycle trainer (SRM, Schoberer Rad Meßtechnik, Jülich, Germany) that had an inbuilt torque meter (SRM PowerMeter professional) recording data into an onboard computer on the cycle trainer (SRM PowerMeter). Each subject warmed up by cycling for 5 min prior to starting the test. The test protocol consisted of 25 min of continuous cycling at near maximal effort. The resistance and cadence were changed every minute in a randomized block design to minimize bias effects of muscle fatigue and temperature on the EMG signals. The cadence ranged between 60 and 130 revolutions per minute (r.p.m.) and a typical protocol can be seen in Fig. 1.

Surface EMG was continuously recorded during the cycle test from the tibialis anterior (TA), medial gastrocnemius (MG), lateral gastrocnemius (LG), soleus (Sol), vastus medialis (VM), rectus femoris (RF), vastus lateralis (VL), biceps femoris long head (BF), semitendinosus (ST) and gluteus maximus (GM). EMG was recorded through bipolar Ag/AgCl electrodes (10 mm diameter, 21 mm spacing) using Biovision amplifiers (Biovision, Wehrheim, Germany). Electrodes were placed in the mid-region of the muscle bellies after the hair had been removed and the skin cleaned with isopropyl alcohol solution. Heart rate was measured using a Polar T31 transmitter and wireless receiver, and the crank position triggered a signal from a reed switch once per revolution. EMG, heart rate and crank position were sampled at 2000 Hz and recorded simultaneously using a 16-bit analog-to-digital convertor (USB-6210, National Instruments, Austin, TX, USA). Initial analysis of the data showed that the maximal power output was achieved at a mean cadence of 95 r.p.m.

In a second test, sagittal plane kinematics were recorded at 300 Hz for the knee and ankle joints using an active optical motion capture system (Optotrak Certus, Northern Digital Inc., Waterloo, Canada). Data were recorded for 20 s after the subject reached a stable cadence of 95 r.p.m. and a 3 min rest was given between conditions with power outputs of 390 and 305 W. Thirty cycles were analysed for each condition to quantify the angular range-of-motion and mean
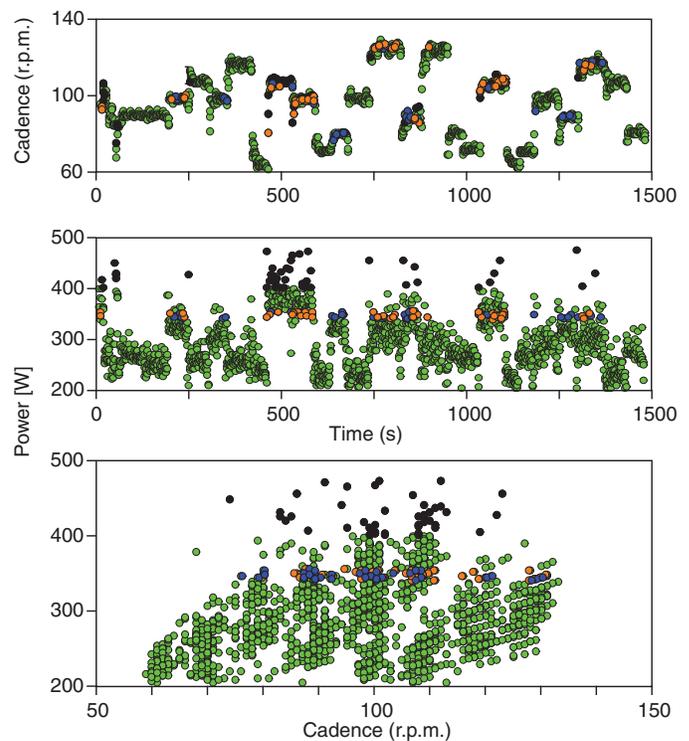

Fig. 1. Experimental protocol for one subject. Dots show the power output and cadence for individual pedal cycles. Pedal cycles that were grouped into the MaxP, High80 and Low80 groups (see text) are shaded black, orange and blue, respectively.

extension velocity for the ankle and knee joints during cycling at these power outputs.

Contractile properties of the muscles
The power output of the knee joint during extension and the ankle joint during plantar flexion were measured during a set of isotonic contractions at maximum effort (Biodex System 2, Biodex Medical Systems Inc., Shirley, NY, USA). Subjects performed sets of 10 isotonic contractions at torques ranging from 1 N m to their isometric maximum voluntary contraction. Ankle power measurements were recorded with the knee angle set to (a) the subject-specific angle that occurred at maximum ankle plantarflexion velocity during the cycle trials (125±8 deg.), and (b) 90 deg. flexion in order to shorten the gastrocnemii and reduce their contribution to the contraction. Two sets were measured for each condition, one incrementing and one decrementing through the isotonic torques to minimize fatigue bias on the mean results; a 45 s rest was given between contractions and a 5 min rest was given between sets.

EMG analysis
EMG signals were quantified by their intensities during each pedal cycle, where the intensity is a close approximation to the power of the signal and was calculated across the frequency band 10–450 Hz using an EMG-specific wavelet analysis (von Tscharner, 2000). The pedal switch was used to partition the EMG intensities for each pedal revolution, starting and finishing with the pedal at top-dead-centre. EMG intensities for each pedal revolution were interpolated to 100 evenly spaced values.

The pedal cadences calculated from the reed switch were cross-correlated with those recorded by the SRM PowerMeter to synchronize the PowerMeter to the EMG signals; the mean

correlation value between these pedal cadences was 0.964±0.019. The mechanical power exerted at the crank was determined for each pedal cycle. The list of power outputs for each pedal revolution was sorted into ascending order of power output. For each subject, the 50 pedal revolutions with the greatest power output were identified. The EMG intensities from every pedal cycle were normalized to the mean of the EMG intensities from these 50 greatest power output cycles for each muscle, and these cycles were referred to as the MaxP group. One-hundred pedal revolutions were identified from the sorted list that had its median value corresponding to a power output that was 80% of the mean power from the MaxP group. These 100 cycles were then ordered by their total EMG intensity (the sum of the EMG intensities from all 10 muscles), and subdivided into 50 cycles that had the lower total EMG intensities, Low80, and 50 cycles with the higher total EMG intensities, High80. Only pedal cycles from the MaxP, High80 and Low80 groups were analysed further.

During maximal exertion activities a large determinate of the metabolic rate is the muscle activity. During cycling the leg muscles generate most of the power output, and so the total EMG intensity across the muscles tested was used as a correlate to the metabolic rate. The mechanical efficiency for the pedal cycle was estimated as the ratio of the crank power to the total EMG intensity, and these efficiencies were normalized to the mean power output for the MaxP condition.

Greater crank powers are needed to accelerate the ergometer when compared with cycling at a steady rate, and in order to test for these effects the acceleration of the ergometer was quantified in terms of the rate of change of the pedal cadence.

The coordination patterns between the muscles were quantified by the relative intensity of the EMG intensities for each pedal cycle. Thus each pedal cycle was represented by 10 values (one per muscle) to describe the coordination and this is termed the EMG intensity profile. Differences in coordination were quantified using principal component (PC) analysis on these 10 values (for all analysed cycles); the PC analysis involved no prior subtraction of the mean coordination pattern and thus the PCs represented the entire signal and not just its variance (Wakeling and Horn, 2009). The effect of the subject, cycle condition, cadence and acceleration on the loading scores for these coordination patterns was tested using analysis of variance. All values in the study are reported as means ± s.e.m.

RESULTS

The same protocol was presented to the subjects, albeit randomized for each subject, and the maximum power output achieved varied with the riding ability and fitness of the subjects. The pedal cycles that were included for analysis in the three groups were distributed across the 25 min cycle test (Fig. 1). From the eight subjects tested the maximum power condition varied between 308.1±2.2 and 436.0±4.0 W and the cadence at which these maximum power outputs occurred varied between 84.6±0.9 and 106.1±0.8 r.p.m. (means ± s.e.m. for the 50 maximum pedal cycles). When considered across all subjects the maximum power output was 381.4±2.2 W (N=400 cycles) and the mean cadence across all conditions was 95.6±0.4 r.p.m. (N=1200 cycles; Fig. 2).

All the muscles tested showed phasic bursts of EMG intensity during the pedal cycle (Fig. 3). The onset and offset timing of these bursts was similar between the mechanical conditions; however, condition-specific variation occurred in the shapes of these bursts when the muscles were active. ANOVA showed a significant association between the total EMG intensity, across all 10 muscles, and the mechanical condition and pedal cadence but there was no
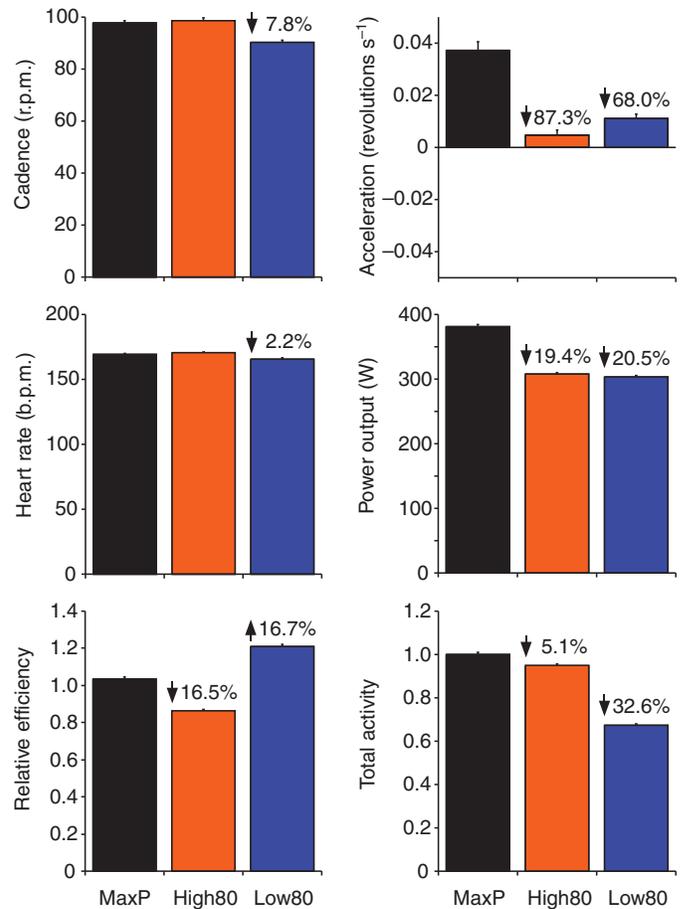

Fig. 2. Differences between the three pedalling conditions. Bars show the mean + s.e.m. for the 400 pedal cycles in each condition. Where ANOVA showed significant differences between the MaxP condition and either the High80 or Low80 condition, the percentage difference from the MaxP value is shown. For all cases ANOVA showed there were significant differences between the High80 and Low80 conditions.

significant effect of the pedal acceleration on the total EMG intensity. Correlation analysis showed that the coefficient of determination between the pedal cadence and total EMG intensity was R^2=0.030.

The general coordination pattern between the muscles was represented by the mean EMG intensity per pedal cycle for the 10 muscles (Fig. 4). The PCs were determined for these EMG intensity profiles (normalized to the total EMG intensity across all 10 muscles). The first four PCs explained 95% of the EMG intensity profiles. ANOVA showed that the loading scores for these four PCs had significant associations with mechanical condition, pedal cadence and pedal acceleration.

The isotonic tests showed that the maximum knee extension power was 104.31±8.90 W, and the power output exceeded 90% of the maximum power output across the range 215.9–366.3 deg. s^{-1}. During cycling the mean angular velocity of the knee during extension was 236.3±4.6 deg. s^{-1} during the 305 W trials and 239.7±4.6 deg. s^{-1} during the 390 W trials: both of these velocities fall within the range that produced greater than 90% knee extension power in the isotonic tests (Fig. 5). Ankle plantarflexion power was measured twice: firstly with the knee fixed at the angle (125 deg. extension) that was observed during maximum ankle extension velocity during cycling and secondly at an angle of 90 deg. When
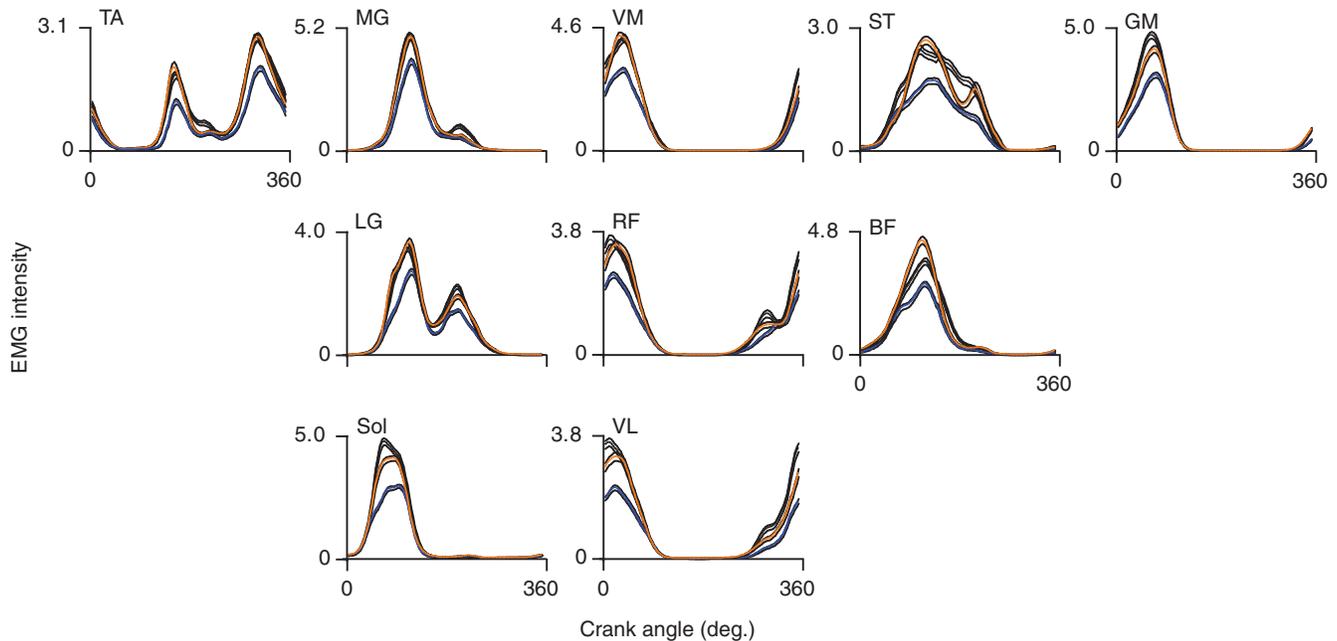
Fig. 3. EMG intensities for a pedal cycle for each muscle. Lines show the mean ± s.e.m. for the normalized EMG intensities for the 400 pedal cycles from each condition. A crank angle of 0 deg. denotes top-dead-centre. The MaxP, High80 and Low80 groups are shaded black, orange and blue, respectively. TA, tibialis anterior; MG, medial gastrocnemius; LG, lateral gastrocnemius; Sol, soleus; VM, vastus medialis; RF, rectus femoris; VL, vastus lateralis; ST, semitendinosus; BF, biceps femoris long head; GM, gluteus maximus.

the knee was held at 125 deg. the maximum ankle plantarflexion power was 48.27±2.26 W, and the power output exceeded 90% of the maximum power output across the range 136.8–273.5 deg. s^{-1}. When the knee was held at 90 deg. the maximum ankle plantarflexion power was 39.20±3.45 W, and the power output exceeded 90% of the maximum power output across the range 120.4–191.3 deg. s^{-1}. During cycling the mean angular velocity of the ankle during plantarflexion was 83.9±12.7 deg. s^{-1} during the 305 W trials and 83.5±12.9 deg. s^{-1} during the 390 W trials: both of these velocities fall too low to produce 90% ankle plantarflexion and indeed they corresponded to 65 and 67% of the maximum power on the isotonic curves, respectively (Fig. 5).

DISCUSSION

This study was designed to investigate the coordination factors during maximal power output cycling. The subjects pedalled at near maximal exertions that they could achieve over the test period, as indicated by the high heart rates recorded (Fig. 2). No subjects could exactly match the required cadence for the whole test despite their efforts, and thus we can be confident that the greatest powers recorded are the maximum possible given the context of the 25 min test. The cycles extracted for analysis were distributed across the whole test period (Fig. 1) and thus would not be biased by fatigue effects. Whilst we could control the initial protocol, there was no control over the cycle-to-cycle variations observed from the subjects. The MaxP and High80 conditions resulted in the same mean cadence; however, the Low80 group had a mean cadence that was 7.8% lower (Fig. 2). Cadence can influence the mechanical power output from muscles as well as the whole body efficiency (Hansen and Sjogaard, 2007; Foss and Hallén, 2004) and so it was included as a covariate in the ANOVA tests; this process statistically isolates its effects so that we can be confident that the reported differences between the groups are independent of fluctuations in cadence.

Additional muscle activity may be required to drive accelerations of the dynamometer, and this was checked by measuring the acceleration of the crank (Fig. 2). The Low80 condition had a greater acceleration than the High80 condition despite having a lower level of muscle activity (Fig. 2); thus, these minimal accelerations did not bias the level of muscle activity. Nonetheless, the crank acceleration was also included as a covariate in the ANOVA tests to statistically isolate its effects from the main differences between the pedalling conditions.

Data from this study showed that during maximum power cycling the ankle plantarflexion velocities during leg extension were too slow for the ankle extensor muscles to generate their maximum power output (Fig. 4). Ankle plantarflexor moments are developed by the gastrocnemii and soleus muscles with the gastrocnemii additionally acting across the knee to result in knee flexion moments. One- and two-joint muscles may play different roles during locomotion: two-joint muscles have been suggested to control the direction of the external limb force (van Ingen Schenau et al., 1992) and this has been supported experimentally in the cat (Kaya et al., 2006). Single-joint muscles have been implicated in power generation (van Ingen Schenau et al., 1992) and in providing stiffness and extensor forces for antigravity functions (Kaya et al., 2006). Zajac and colleagues (Zajac, et al., 2002) cautioned against placing functional interpretations for individual muscles because all muscles contribute to segmental accelerations of the whole body. Indeed, the soleus and gastrocnemii have been suggested to have similar functions during cycling when determined through simulation studies (Zajac et al., 2002); however, these studies assumed that the muscle activity was similar between these muscles. In contrast, experimental observations show that muscle activity varies between these muscles when the mechanical demands of cycling are varied (Wakeling and Horn, 2009) and this indicated that the soleus and gastrocnemii make different contributions to the whole limb performance.
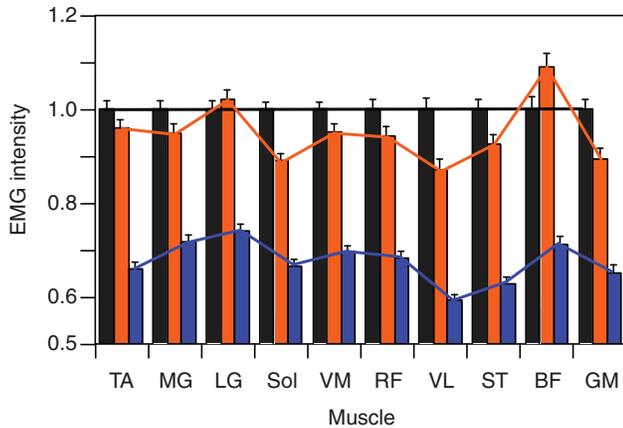
Fig. 4. EMG intensity profiles showing muscle coordination. The MaxP, High80 and Low80 groups are shaded black, orange and blue, respectively. EMG intensities have been normalized to their values for the MaxP condition. Bars show the means + s.e.m. for the 400 pedal cycles in each condition.

Fig. 5. Power output for the knee (A) and ankle (B) joints. Points and ellipses show the mean ± s.e.m. power output at a series of angular velocities measured on an isotonic dynamometer; least-squares third order polynomial curves fitted to these points are shown. Horizontal lines show the range of angular velocities that would achieve at least 90% of the maximum power output. Vertical arrows show the joint angular velocities during cycling at crank powers of 305 and 390 W; the apex of the arrow shows the mean angular velocity, and the edges of each arrow are 1 s.e.m. from the mean. For the ankle joint, the solid lines show isotonic results for ankle plantar flexion when the knee was held at its mean angle during cycling; the dashed lines show results with the knee held at 90 deg.

The soleus muscle has a greater proportion of slow muscle fibres than the gastrocnemii (Johnson et al., 1973), and so it is possible that this muscle was operating at velocities sufficient for maximum power output even when the gastrocnemii were not. However, one set of dynometric tests held the knee at a 90 deg. flexion in order to reduce the length of the gastocnemii and reduce their contribution to ankle plantarflexion. Even during these measurements the ankle plantarflexion velocities during cycling were only 53% of the plantarflexion velocity required for maximum power output. Therefore, even though the limb is operating at maximum power output, the muscles do not necessarily have to operate at their individual maximum power output.

For a muscle to produce maximal power output it must produce a large force during shortening and minimal force while it is being stretched. High levels of concentric force are achieved with large muscle activations, and provided the contraction duration is long enough to allow full activation to be reached then the muscle will be fully active when it is producing its maximal power output. For a muscle operating at the same range of lengths and shortening velocities, the power output will be proportional to the level of activation. The data from this study show that when the limb is operating at 80% of its maximal power output this can be achieved with very different levels of muscle activation (Fig. 4) for all the muscles in general, and also more specifically for the muscles that have been implicated in power generation during cycling [such as the VM and VL (Ryan and Gregor, 1992)]. Furthermore, the limb power does not correlate with the levels of activity when considered on a cycle-by-cycle basis ($R^2<0.08$ for VL and VM, mean correlation $R^2=0.06$ when considered for all 10 muscles). Additionally, substantial increases in limb power output can be achieved (24% from the High80 to the MaxP conditions) when the increases in muscle activity are more limited (5%, Fig. 2). These results indicate that the levels of whole limb power output were poorly associated with the levels of activity in the individual muscles, *per se*, and so the individual muscles do not necessarily produce maximum power output when the limb is generating its maximum power. The maximum power output from a limb can, therefore, be achieved without maximum power output being produced from individual muscles.

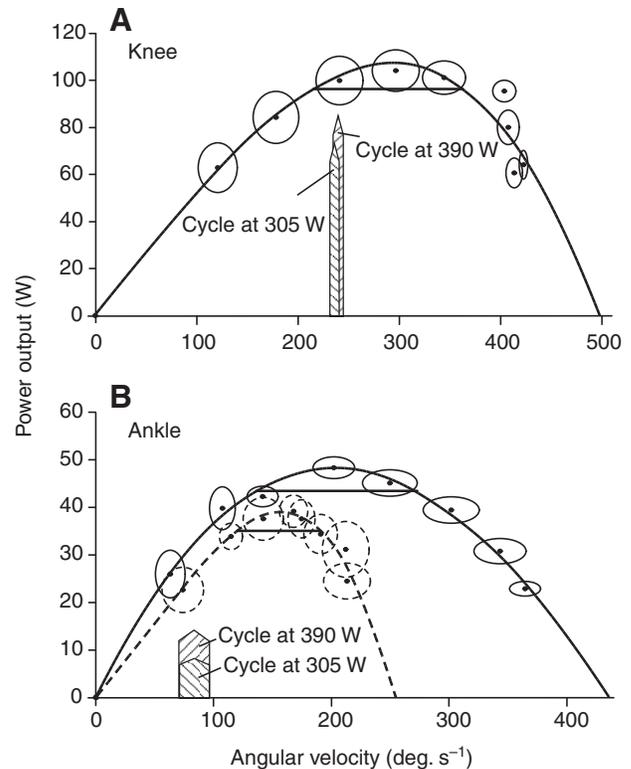The timing of onset and offset of muscle activity was strongly conserved between test conditions for all muscles (Fig. 3). Changes in the timing of activity relative to pedal position have previously been reported for cycling when the cadence is varied (Neptune et al., 1997; Wakeling and Horn, 2009) due to the electromechanical delay representing an increasingly large fraction of the cycle duration at higher pedalling rates (Neptune et al., 1997). However, in this study the cadence was very similar between the three test conditions, and so the muscle activity occurred at similar times relative to each pedal cycle. The EMG intensities did vary, however, in their relative levels between the muscles. These EMG intensity profiles can be considered as the coordination pattern between the muscles and these did significantly vary between the test conditions. Such variation is not the result of cross-talk between the electrodes because (a) cross-talk would instead be correlated between the muscles, and (b) cross-talk has previously been shown to account for <4% of the signals for similar protocols (Wakeling, 2009). Previous studies have shown that muscle coordination varies with mechanical demand (both torque and cadence) during cycling (Wakeling and Horn, 2009); and here we show that the same mechanical output from the limb can be achieved with different patterns of coordination.

Muscle efficiency is the ratio of the mechanical power output to the metabolic cost of the contraction. Maximum muscle efficiencies have been reported across a range of 15–29% of the maximum

intrinsic shortening speed for different muscles (Hill, 1964; Woledge et al., 1985; He et al., 2000). This study has shown that not all muscles shorten at velocities appropriate for maximal power production during these cycling tasks, and similarly it is likely that not all muscles were shortening at velocities that would have maximized their mechanical efficiency. However, the three cycle conditions tested had similar pedal cadences, the joint range-of-motions had similar angular excursions that were constrained by the bike geometry, and so it is likely that similar muscle efficiencies occurred between the conditions. The efficiency for producing mechanical power at the joints depends in part on the level of co-contractions of the antagonistic muscles. Co-contractions of single-joint muscles may result in reduced joint power for an increased metabolic cost of the muscle contractions. Nevertheless, co-contractions of two-joint muscles may be necessary for controlling the direction of the external force (van Ingen Schenau et al., 1992). For the pedalling task the external force only needs to be tangential to the direction of the pedal velocity; components of force in any other direction are not necessary and therefore contribute to pedalling inefficiencies. The direction of the pedalling force has been shown to deviate considerably from the optimal direction during cycling (Patterson et al., 1983; Sanderson, 1991; Zameziati et al., 2006; Hug et al., 2008), indicating that the muscle coordination pattern may not be appropriate for delivering the necessary external force directions for maximizing pedalling efficiency.

The overall efficiency of the cycling is the ratio of the mechanical power output at the crank to the metabolic cost of the task. Pedalling with ineffective external forces has been shown to reduce the overall efficiency during cycling (Zameziati et al., 2006). Vigorous activity can result in the metabolic rate reaching 20 times the resting levels (Young et al., 1959) with most of this increase being due to skeletal muscle contractions. During cycling the muscles of the leg are responsible for generating the majority of the mechanical power and so we have used the total EMG intensity as a proxy of the metabolic cost of the cycling. The Low80 and High80 conditions resulted in the same mechanical power output despite very different levels of EMG intensity, and so the Low80 condition occurred with approximately 40% greater efficiency than the High80 condition (Fig. 2). The relative timing of the muscle activity within the pedal cycles was similar for these two groups (Fig. 3) but they did differ in their EMG intensity profiles (Fig. 4) and thus muscle coordination. Changes in muscle coordination between the pedalling conditions are thus associated with differences in the efficiency of power production by the limb.

During steady, level locomotion the skeletal muscles must generate the power required for the movement and thus the locomotor performance cannot exceed the power available from the muscles. The results from this study show that the maximum power output from the limbs occurs when neither all joints nor all muscles are operating at their individual maximum power output. Instead, both the power output and mechanical efficiency of the limb are limited by the coordination pattern of the muscles.

SUMMARY

(1) When a limb is operating at maximal power output, not all its joints need rotate at velocities where their maximum power output can be achieved.
(2) Even muscles that are shortening at their optimal speed for maximal power production may not be fully activated to achieve high limb power.
(3) The same mechanical output from the limb can be achieved with different patterns of coordination.

(4) Increases in muscle activity can lead to decreases in efficiency with no increase in power output if the coordination is inappropriate.
(5) Power output from the limb cannot exceed the maximum power that can be produced by the muscles, but does seem to be limited by the coordination patterns of those muscles.

REFERENCES

Foss, O. and Hallén, J. (2004). The most economical cadence increases with increasing workload. *Eur. J. Appl. Physiol.* **92**, 443-451.
Gregor, R. J., Cavanagh, P. R. and LaFortune, M. (1985). Knee flexor moments during propulsion in cycling – a creative solution to Lombard's paradox. *J. Biomech.* **18**, 307-316.
Hansen, E. A. and Sjogaard, G. (2007). Relationship between efficiency and pedal rate in cycling: significance of internal power and muscle fiber type composition. *Scand. J. Med. Sci. Sports* **17**, 408-414.
He, Z.-H., Bottinelli, R., Pellegrino, M. A., Ferenczi, M. A. and Reggiani, C. (2000). ATP consumption and efficiency of human single muscle fibers with different myosin isoform composition. *Biophys. J.* **79**, 945-961.
Hill, A. V. (1964). The efficiency of mechanical power development during muscular shortening and its relation to load. *Proc. R. Soc. B* **159**, 319-324.
Hug, F. and Dorel, S. (2009). Electromyographic analysis of pedaling: a review. *J. Electromyogr. Kinesiol.* **19**, 182-198.
Hug, F., Drouet, J. M., Champoux, Y., Couturier, A. and Dorel, S. (2008). Interindividual variability of electromyographic patterns and pedal force profiles in trained cyclists. *Eur. J. Appl. Physiol.* **104**, 667-678.
Johnson, M. A., Polgar, J., Weightman, D. and Appleton, D. (1973). Data on the distribution of fibre types in thirty-six human muscles. An autopsy study. *J. Neurol. Sci.* **18**, 111-129.
Josephson, R. K. (1999). Dissecting muscle power output. *J. Exp. Biol.* **202**, 3369-3375.
Kaya, M., Leonard, T. R. and Herzog, W. (2006). Control of ground reaction forces by hindlimb muscles during cat locomotion. *J. Biomech.* **39**, 2752-2766.
Kushermick, M. J. and Davies, R. E. (1969). The chemical energetics of muscle contraction. II. The chemistry, efficiency and power of maximally working sartorius muscles. *Proc. R. Soc. Lond. B* **174**, 315-353.
Lieber, R. L. and Fridén, J. (2000). Functional and clinical significance of skeletal muscle architecture. *Muscle Nerve* **11**, 1647-1666.
Lombard, W. P. (1903). The action of two-joint muscles. *Am. Physiol. Ed. Rev.* **8**, 141-145.
Neptune, R. R. and Herzog, W. (2000). Adaptation of muscle coordination to altered task mechanics during steady-state cycling. *J. Biomech.* **33**, 165-172.
Neptune, R. R., Kautz, S. A. and Hull, M. L. (1997). The effect of pedaling rate on coordination in cycling. *J. Biomech.* **30**, 1051-1058.
Patterson, R. P., Pearson, J. L. and Fisher, S. V. (1983). The influence of flywheel weight and pedalling frequency on the biomechanics. *Ergonomics* **26**, 659-668.
Ryan, M. M. and Gregor, R. J. (1992). EMG profiles of lower extremity muscles during cycling at constant workload and cadence. *J. Electromyogr. Kinesiol.* **2**, 69-80.
Sanderson, D. J. (1991). The influence of cadence and power output on the biomechanics of force application during steady-rate cycling in competitive and recreational cyclists. *J. Sports Sci.* **9**, 191-203.
Sargeant, A. J., Hoinville, E. and Young, A. (1981). Maximum leg force and power output during short-term dynamic exercise. *J. Appl. Physiol.* **51**, 1175-1182.
Swoap, S. J., Caiozzo, V. J. and Baldwin, K. M. (1997). Optimal shortening velocities for in situ power production of rat soleus and plantaris muscles. *Am. J. Physiol.* **273**, C1057-C1063.
Tihanyi, J., Apor, P. and Fekete, Gy. (1982). Force-velocity-power characteristics and fiber composition in human knee extensor muscles. *Eur. J. Appl. Physiol.* **48**, 331-343.
van Ingen Schenau, G. J., Boots, P. J. M., de Groot, G., Snackers, R. J. and van Woensel, W. W. L. M. (1992). The constrained control of force and position in multi-joint movements. *Neuroscience* **46**, 197-207.
von Tscharner, V. (2000). Intensity analysis in time-frequency space of surface myoelectric signals by wavelets of specified resolution. *J. Electromyogr. Kinesiol.* **10**, 433-445.
Wakeling, J. M. (2009). The recruitment of different compartments within a muscle depends on the mechanics of the movement. *Biol. Lett.* **5**, 30-34.
Wakeling, J. M. and Horn, T. (2009). Neuromechanics of muscle synergies during cycling. *J. Neurophysiol.* **101**, 843-854.
Woledge, R. C., Curtin, N. A. and Homsher, E. (1985). *Energetic Aspects Of Muscle Contraction*, 357pp. London: Academic Press.
Young, D. R., Mosher, R., Erve, P. and Spector, H. (1959). Energy metabolism and gas exchange during treadmill running in dogs. *J. Appl. Physiol.* **14**, 834-838.
Zajac, F. E., Neptune, R. R. and Kautz, S. A. (2002). Biomechanics and muscle coordination of human walking. Part I: Introduction to concepts, power transfer, dynamics and simulations. *Gait Posture* **16**, 215-232.
Zameziati, K., Mornieux, G., Rouffet, D. and Belli, A. (2006). Relationship between the increase of effectiveness indexes and the increase of muscular efficiency with cycling power and physiological responses to bicycle exercise. *Eur. J. Appl. Physiol.* **96**, 274-281.
Zoladz, J. A., Rademaker, A. C. H. J. and Sargeant, A. J. (2000). Human muscle power generating capability during cycling at different pedalling rates. *Exp. Physiol.* **85**, 117-124.