

Muscle fiber type effects on energetically optimal cadences in cycling

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Abstract

Fast-twitch (FT) and slow-twitch (ST) muscle fibers vary in their mechanical and energetic properties, and it has been suggested that muscle fiber type distribution influences energy expenditure and the energetically optimal cadence during pedaling. However, it is challenging to experimentally isolate the effects of muscle fiber type on pedaling energetics. In the present study, a modeling and computer simulation approach was used to test the dependence of muscle energy expenditure on pedaling rate during submaximal cycling. Simulations were generated using a musculoskeletal model at cadences from 40 to 120 rev min⁻¹, and the dynamic and energetic properties of the model muscles were scaled to represent a range of muscle fiber types. Energy expenditure and the energetically optimal cadence were found to be higher in a model with more FT fibers than a model with more ST fibers, consistent with predictions from the experimental literature. At the muscle level, mechanical efficiency was lower in the model with a greater proportion of FT fibers, but peaked at a higher cadence than in the ST model. Regardless of fiber type distribution, mechanical efficiency was low at 40 rev min⁻¹, increased to a broad plateau between 60 and 100 rev min⁻¹, and decreased substantially at 120 rev min⁻¹. In conclusion, muscle fiber type distribution was confirmed as an important determinant of the energetics of pedaling. © 2005 Elsevier Ltd. All rights reserved.

Keywords: Bicycling; Pedaling rate; Biomechanics; Musculoskeletal model; Computer simulation

1. Introduction

Differences in the mechanical and energetic properties of isolated mammalian slow-twitch (ST) and fast-twitch (FT) muscles, motor units, and muscle fibers have been well documented (Bottinelli and Reggiani, 2000; Burke, 1994; Rall, 1985). In general, ST muscles are slower, less powerful, and more economical at force generation than FT muscles from the same species. Furthermore, peak efficiency of ST muscle fibers occurs at slower shortening speeds than in FT fibers (Barclay, 1994; Bottinelli and Reggiani, 2000). In humans, the limb muscles are heterogeneous with respect to fiber type distribution (Johnson et al., 1973), but mechanical and energetic

descriptors of muscular performance seem to scale quite predictably with the proportions of FT and ST muscle fibers (Coyle et al., 1979; Coyle et al., 1992; Thorstensson et al., 1976).

Bicycle pedaling has been used as an experimental paradigm in numerous investigations of fiber type-related issues, and a few of these studies particularly exemplify how muscle fiber type composition may affect energy expenditure and the energetically optimal cadence during pedaling (Coyle et al., 1992; Hansen et al., 2002; Hintzy et al., 1999). Coyle et al. (1992) found the percentage of ST muscle fibers in vastus lateralis to be positively correlated with gross ($r = 0.75$) and delta ($r = 0.85$) efficiency in endurance cyclists, and a similar relationship ($r = 0.61$) for gross efficiency was reported by Hansen and colleagues (2002). The four subjects in Coyle et al. (1992) with the highest percentage of FT muscle fibers (63% FT) expended 14% more metabolic

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energy than the four subjects with the lowest percentage of FT fibers (27% FT), at the same mechanical power output and cadence. Supporting evidence suggested that the between-subject differences in efficiency could not be explained by other factors such as pedaling technique (Coyle et al., 1991), and similar results were found in a different motor tasks (Coyle et al., 1992).

More recently, Hintzy et al. (1999) reported a positive relationship ($r = 0.75$) between the energetically optimal cadence and the cadence at which short-term power output was maximized (maximal power cadence) in three groups of trained noncyclists. In addition, the energetically optimal cadence was significantly higher in the group of explosively trained athletes ($60.8 \text{ rev min}^{-1}$) than in the endurance-trained group ($54.0 \text{ rev min}^{-1}$). Hintzy and colleagues did not assess muscle fiber type directly, however, subjects with higher maximal power cadences tend to have a greater proportion of FT muscle fibers (Hansen et al., 2002; Hautier et al., 1996), suggesting a positive relationship between energetically optimal cadence and the percentage of FT fibers. Thus, the differences in submaximal energy expenditure between subjects, and the cadences at which energy is minimized can presumably be explained largely by muscle fiber type distribution.

These findings are notable in that they point to the role of fundamental muscle properties in determining the energetics of pedaling, rather than experience or training history. In contrast, others have suggested that during training cyclists adapt to become more efficient at pedaling, often with the adoption of a relatively high cadence (Coast and Welch, 1985; Hagberg et al., 1981). While muscle fiber type distribution may influence energy output and optimal cadence during pedaling, it is difficult to determine the direct influence of fiber type distribution per se. Quantification of fiber type is usually based on a small number of biopsies, typically obtained from just one muscle. An alternative approach to study the effects of fiber type distribution on pedaling energetics is through musculoskeletal modeling and computer simulation. Modeling and simulation are common tools for investigating the mechanics and control of pedaling (Neptune and Hull, 1999; Raasch et al., 1997; van Soest and Casius, 2000), and the use of a model of muscle heat production (Umberger et al., 2003) further allows the energetics of pedaling to be investigated. Computer simulation can be an especially powerful tool, as it provides estimates of many important quantities not accessible in an experimental setting (e.g., muscle forces, muscle energy expenditure).

The objective of the present study was to determine the effects of muscle fiber type distribution on muscle and whole-body energetics during submaximal pedaling using a modeling and simulation approach. This objective was met using two musculoskeletal models that reflected a realistic range of fiber types for human

lower limb muscles. The specific quantities investigated were the cadences at which submaximal energy expenditure was minimized, as well as the mechanical and energetic output of the lower limb muscles across a range of cadences. The only difference between the two models was muscle fiber type distribution. Thus, it allowed for an assessment of the relative effect of this factor on submaximal pedaling performance.

2. Methods

Two models of human bicycle pedaling were developed that were identical in every way except for the mechanical and energetic properties of the muscles. One model had muscle parameter values that were consistent with a high percentage of FT fibers (FT model), while the other model reflected a low percentage of FT muscle fibers (ST model). Muscle energy expenditure was estimated using a model in which energy liberation depended on muscle fiber type distribution.

2.1. Skeletal and bicycle models

A model of the bicycle and rider was developed that was similar to existing models (Neptune and Hull, 1998; Raasch et al., 1997; van Soest and Casius, 2000). Nine rigid body segments represented the trunk, thighs, shanks, feet, bicycle frame, and crank. The skeletal segments articulated at six frictionless revolute joints representing the right and left hip, knee, and ankle joints. The foot segments articulated with the ends of the crank arm via two frictionless revolute joints, and the inferior aspect of the trunk segment (approximating the hip joint) was coincident with the superior aspect of the bicycle frame segment (representing the bicycle seat). The bicycle frame and trunk segments were fixed in space, and motion was constrained to the sagittal plane. The resulting model had three rotational degrees of freedom, which were the crank angle and two pedal angles. The dynamic load at the crank was modeled on a standard road bicycle with 52/20 gearing (Fregly et al., 2000). Further details regarding the skeletal and bicycle models can be found in Umberger (2003).

2.2. Muscle model

The skeletal/bicycle model was driven by 24 musculotendon actuators (Table 1) that represented the major sagittal plane muscles of the lower limb. A modified version (Umberger et al., 2003) of a Hill-type muscle model (van Soest and Bobbert, 1993) accounted for the dependence of muscle force on contractile element (CE) length, velocity, and activation. The model incorporated between-muscle differences in CE mechanical properties (e.g., shape of the force–velocity curve, maximal short-

Table 1

Parameter values for the muscle model that were the same regardless of muscle fiber type distribution

Muscle	Mass (kg)	Penn. (deg)	$L_{CE(OPT)}$ (m)	PCSA (m^2)	F_{MAX} (N)	L_{SLACK} (m)	Width
Soleus ^a	0.587	25	0.055	0.0179	3127	0.255	0.80
Other PFs ^a	0.395	10	0.039	0.0096	2389	0.349	0.56
Gastrocnemius	0.326	14	0.055	0.0060	1384	0.376	0.61
Vasti	2.160	4	0.086	0.0237	5925	0.148	0.55
Rectus femoris	0.540	5	0.084	0.0061	1118	0.345	0.76
Glutei	1.973	3	0.145	0.0128	2335	0.143	0.77
Medial hams ^b	0.905	13	0.109	0.0078	1463	0.373	0.75
Biceps fem(lh) ^b	0.351	0	0.109	0.0030	546	0.392	0.78
Biceps fem(sh)	0.262	23	0.173	0.0014	267	0.083	0.75
Iliacus ^c	0.394	7	0.100	0.0037	704	0.091	0.74
Psoas major ^c	0.447	8	0.104	0.0041	811	0.136	0.70
Dorsiflexors	0.615	7	0.082	0.0059	1466	0.235	0.49

Penn. is muscle fiber pennation angle and $L_{CE(OPT)}$ is contractile element optimal length. PCSA is physiological cross-sectional area and F_{MAX} is contractile element maximal isometric force. PCSA, F_{MAX} , and mass were determined together as described in Umberger et al. (2003). L_{SLACK} is series elastic element slack length and Width is the relative spread of the normalized force length curve. Both were determined for each muscle such that the model reproduced experimental isometric torque curves (Umberger, 2003).

Note: muscles with the same superscript were considered to be part of the same group, and received the same excitation signal.

Table 2

Parameter values for the muscle model that depended on muscle fiber type distribution

Muscle	Fast-twitch model					Standard model					Slow-twitch model				
	%FT	A_{REL}	B_{REL}	τ_{ACT}	τ_{DEA}	%FT	A_{REL}	B_{REL}	τ_{ACT}	τ_{DEA}	%FT	A_{REL}	B_{REL}	τ_{ACT}	τ_{DEA}
Soleus	35	0.24	2.9	63	74	20	0.18	2.2	70	83	5	0.12	1.4	78	92
Other PFs	50	0.30	3.6	55	65	40	0.26	3.1	60	71	30	0.22	2.6	65	77
Gastrocnemius	60	0.34	4.1	50	59	50	0.30	3.6	55	65	40	0.26	3.1	60	71
Vasti	60	0.34	4.1	50	59	50	0.30	3.6	55	65	40	0.26	3.1	60	71
Rectus femoris	75	0.40	4.8	43	50	65	0.36	4.3	48	56	55	0.32	3.8	53	62
Glutei	70	0.38	4.6	45	53	45	0.28	3.4	58	68	20	0.18	2.2	70	83
Medial hams	55	0.32	3.8	53	62	35	0.24	2.9	63	74	15	0.16	1.9	73	86
Biceps fem(lh)	55	0.32	3.8	53	62	35	0.24	2.9	63	74	15	0.16	1.9	73	86
Biceps fem(sh)	55	0.32	3.8	53	62	35	0.24	2.9	63	74	15	0.16	1.9	73	86
Iliacus	70	0.38	4.6	45	53	50	0.30	3.6	55	65	30	0.22	2.6	65	77
Psoas major	70	0.38	4.6	45	53	50	0.30	3.6	55	65	30	0.22	2.6	65	77
Dorsiflexors	40	0.26	3.1	60	71	25	0.20	2.4	68	80	5	0.12	1.4	78	92

%FT is percentage of fast-twitch muscle fibers, A_{REL} and B_{REL} are normalized Hill constants (a/F_{MAX} and $b/L_{CE(OPT)}$), and τ_{ACT} and τ_{DEA} are the activation and deactivation time constants in ms. Fiber type composition was based on Johnson et al. (1973) and all other values were determined from fiber type using procedures described in Umberger et al. (2003).

ening velocity) that depend on fiber type, or change with increasing activation to reflect the progressive recruitment of faster motor units. Total energy output for each muscle was calculated from the sum of mechanical power and the rate of heat production (Umberger et al., 2003). Mechanical power output was determined from CE force and velocity, and heat rate depended on CE length, velocity, excitation/activation, and muscle fiber type distribution. For identical contractile conditions, the mass-specific energy rate would always be higher for a muscle with a greater percentage of FT fibers.

Fiber type data from Johnson et al. (1973) were used to define three models: a standard model, a FT model, and a ST model. The proportions of FT and ST muscle fibers in the standard model were based on group mean

data from Johnson and colleagues, while the proportions of FT fibers in the other two models represented approximately two standard deviations above (FT model) and two standard deviations below (ST model) the mean value for each muscle (Table 2). Despite the small sample size in Johnson et al. ($n = 6$), model fiber type distributions were consistent with muscle biopsy data on sprint athletes (FT model), endurance athletes (ST model), and untrained subjects (standard model) (e.g., Clarkson et al., 1980; Costill et al., 1976; Elder et al., 1982; Gollnick et al., 1972). While individual subjects from any group can certainly have extreme fiber type distributions, our intention was to define models where the percentages of FT and ST fibers represented reasonable group means for the three

different populations. In the present study, the focus was on the FT and ST models.

The entire sequence of muscle excitation–contraction coupling was modeled as a first-order process (He et al., 1991), with activation and deactivation time constants (Table 2) based on muscle fiber type distribution (Umberger et al., 2003). The control signals to the muscles were represented by triple block-shaped excitation profiles described by seven parameters that encoded when (switching times) and by how much (amplitude change) excitation changed during a pedal cycle. Thus, the control signals could take on three independent levels during a period of excitation. By assuming that the neural inputs to each leg were the same, but 50% out of phase, and by grouping certain muscles to receive the same excitation signal (Table 1), the cycling model could be controlled by specifying the values of 63 input parameters (nine muscle groups \times seven parameters per muscle group).

2.3. Simulations

The equations of motion for the bicycle-plus-rider system were generated using DADS multibody modeling software (LMS International, Leuven, Belgium). Simulations of submaximal pedaling were generated for both models at average cadences of 40, 60, 80, 100, and 120 rev min⁻¹, with an average power output of 200 W. Muscle excitation patterns (switching times and amplitudes) were found using dynamic optimization (Bremermann, 1970; Winters et al., 1984) to produce forward pedaling by minimizing the sum of squared differences between simulated and experimental crank torque and pedal angle data, while simultaneously minimizing muscle energy expenditure to produce an economical pedaling pattern. The objective function was similar to one investigated by Neptune and Hull (1998), but added an energy component similar to Raasch and Zajac (1999). The three criteria were weighted such that they made approximately equal contributions to the objective function. Simulations were performed over three pedal revolutions, with time and power constraints enforced on the third revolution. Only this final pedal revolution was subjected to further analysis.

2.4. Experimental procedures

Experimental crank torque and pedal angle data were collected for use in the dynamic optimization problem. Electromyography (EMG) data were also collected for comparison with the timing of simulated muscle activity bursts. The experimental data were obtained from a healthy male subject (height = 1.85 m; mass = 74.2 kg; age = 26 yr) who pedaled on a bicycle ergometer at the same cadences and power output as in the simulations. Pedal force and angle data were recorded (1000 Hz)

using two pedal dynamometers (Newmiller et al., 1988), while surface EMG data were simultaneously sampled using an EMG amplifier (Bortec Biomedical, Calgary, AB, Canada) from eight muscles in the right lower limb (soleus, gastrocnemius, tibialis anterior, vastus lateralis, rectus femoris, gluteus maximus, medial hamstrings, and iliopsoas). Signals from iliopsoas were recorded using a small electrode pair that was placed halfway between the anterior superior iliac spine and pubic tubercle, and approximately 2 cm distal to the inguinal ligament. A series of isometric contractions associated with different joint actions (hip flexion, lumbar flexion, hip adduction, etc.) were then performed to insure a minimum of cross talk from neighboring muscles.

2.5. Analysis

The quantities of interest in the current study were the cadences at which muscle and whole-body rates of energy expenditure were minimized for the two different models. Muscle energy rate was calculated by summing the energy (heat + work) expended by all 24 lower limb muscles over the last pedal cycle. Muscle mechanical efficiency was calculated by dividing the mechanical work summed over the leg muscles, by the total leg muscle energy expenditure. The total muscle mechanical work included both the external work, and any so-called “internal” work done to move the legs. To estimate whole-body energy liberation, energy expended by the “rest of the body” (residual body mass) must be known. Residual body mass (57.1 kg) was determined by subtracting the mass of the lower limb muscles (17.9 kg) from the mass of the entire body (75 kg), and was assigned an energy rate that increased quadratically with cadence. Based on data from subjects pedaling against zero load (Böning et al., 1984; Gaesser and Brooks, 1975; Hagberg et al., 1981; Seabury et al., 1977) the energy rates for the residual body mass at 40, 60, 80, 100, and 120 rev min⁻¹ were 2.0, 2.4, 3.2, 4.5, and 6.6 W kg⁻¹, respectively.

3. Results

After optimization of the muscle excitation parameters, both the FT and ST models were able to generate pedaling at the target power and cadences (within $\pm 1\%$) while reproducing the major kinematic and kinetic features of human cycling (Fig. 1). Root mean square errors between simulation and experimental data ranged from 0.63° to 2.58° for pedal angle and 0.99 to 4.66 N m for crank torque. Timings of muscle activity bursts, based on the optimized excitation profiles, were also in reasonable temporal agreement with experimental data (Fig. 2).

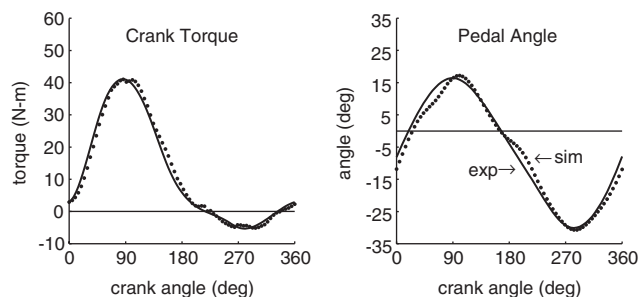


Fig. 1. Comparison of crank torque and global pedal angle between simulation (dotted lines) and experimental data (solid lines). Over the whole pedal cycle there was good agreement between the simulated and target data. The pedal kinematics, though, were not quite as smooth as the experimental data. Results are shown for the FT model at the 80 rev min^{-1} condition. Root mean square deviations between simulated and experimental data over all cadence conditions for both models ranged from $0.99\text{--}4.66 \text{ N m}$ for crank torque and $0.63\text{--}2.58^\circ$ for pedal angle.

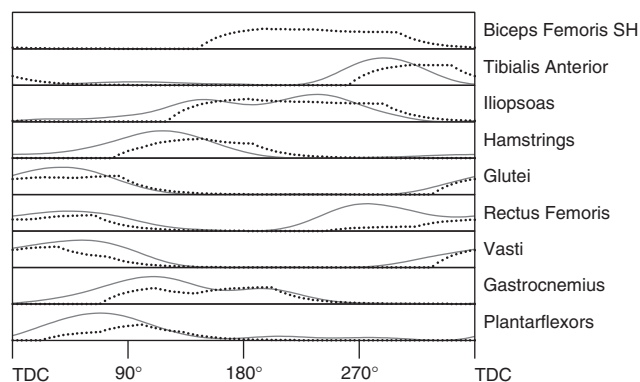


Fig. 2. Comparison between model muscle activity bursts (dotted lines) based on the optimized excitation parameters, and experimental EMG data (gray lines) for submaximal pedaling. For most muscles there was good agreement in the timing of muscle activity. Results are shown for the FT model at the 80 rev min^{-1} condition, but similar results were obtained for all conditions. No EMG data were available for the short head of muscle biceps femoris.

The whole-body rates of energy expenditure for the two models are shown in Fig. 3, contrasted with group mean data from several studies in the literature (Böning et al., 1984; Coast and Welch, 1985; Marsh and Martin, 1997; Seabury et al., 1977; Takaishi et al., 1998). Rates of oxygen consumption have been converted to watts where necessary using an energy equivalent for oxygen of $20.2 \text{ kJ L}^{-1} \text{ O}_2$ (Weir, 1949), based on a respiratory exchange ratio of 0.85 (Böning et al., 1984). The magnitude of energy expenditure for the two models was generally comparable to experimental values, with energy expended by the FT model exceeding that of the ST model by approximately 15–30% over the range of cadences. The cadences at which energy expenditure was predicted to be minimized were 64 rev min^{-1} for the FT model and 55 rev min^{-1} for the ST model. The leg

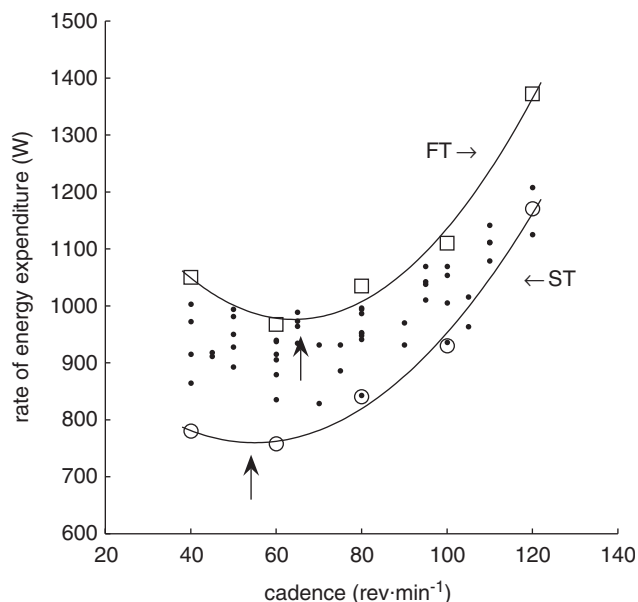


Fig. 3. Whole-body energy expenditure during simulated pedaling at 200 W. Energy expenditure for the FT (open squares) and ST models (open circles), is contrasted with group mean data from several studies (small black circles—sources are given in the text). Vertical arrows indicate the predicted energy minima for the FT (64 rev min^{-1}) and ST (55 rev min^{-1}) models.

muscles dominated the total energy expenditure (58–86% of the total) for both models (Fig. 4), although the contribution of the residual body mass was substantial at higher cadences. The cadences predicted to maximize muscle mechanical efficiency (Fig. 5) were higher for both the FT (84 rev min^{-1}) and ST (72 rev min^{-1}) models than the cadences minimizing whole-body energy expenditure.

4. Discussion

The simulations demonstrated that varying muscle fiber type distribution changes energetically optimal pedaling rate in a manner consistent with differences observed in the literature. The energetically optimal cadences (FT: 64 rev min^{-1} , ST: 55 rev min^{-1}) were comparable to experimental values (Coast and Welch, 1985; Marsh and Martin, 1997; Seabury et al., 1977), and the 9 rev min^{-1} difference between FT and ST models was similar to the 7 rev min^{-1} deviation reported by Hintzy et al. (1999). While these results do not preclude the possibility that other neuromuscular factors might influence pedaling mechanics and energetics, they do point to the important role that the genetically determined muscle fiber type distribution plays in pedaling performance.

Whole-body rates of metabolic energy expenditure calculated for the FT and ST models (Fig. 3) were similar to values determined experimentally (Böning

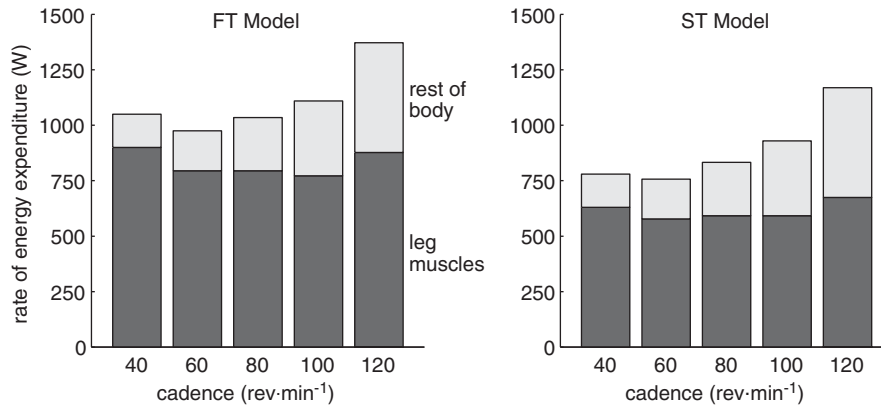


Fig. 4. Contributions of the leg muscles and the rest of the body to the total metabolic energy expenditure in simulated submaximal cycling. For both models, the energy expended by the leg muscles dominated the total energy expenditure. Furthermore, muscle energy consumption exhibited a different trend across cadences than whole-body energy expenditure. After initially decreasing from 40 to 60 rev min⁻¹, muscle energy expenditure did not increase substantially until 120 rev min⁻¹. Whole-body energy expenditure, on the other hand, increased steadily from 60 to 120 rev min⁻¹.

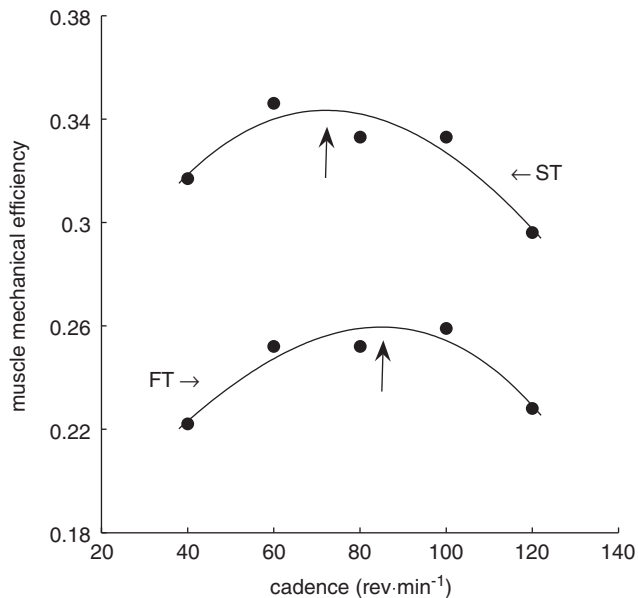


Fig. 5. Muscle mechanical efficiency during simulated pedaling at 200 W. Mechanical efficiency, defined as work/(heat + work), of the lower limb muscles was lower in the FT model, but peaked at a higher cadence. Vertical arrows indicate predicted efficiency maxima for the FT (84 rev min⁻¹) and ST (72 rev min⁻¹) models.

et al., 1984; Coast and Welch, 1985; Marsh and Martin, 1997; Seabury et al., 1977; Takaishi, et al., 1998). If the results at 80 rev min⁻¹ are expressed in terms of gross efficiency ($e_g = 200 \text{ W} \times \text{energy rate}^{-1}$), then there was excellent agreement between the gross efficiency for the FT model ($e_g = 0.193$) and the predicted gross efficiency for subjects with 60% FT fibers in vastus lateralis ($e_g = 0.196$; Coyle et al., 1992). Gross efficiency for the ST model ($e_g = 0.238$) was higher than would be predicted for subjects with 40% FT fibers in vastus lateralis ($e_g = 0.209$; Coyle et al., 1992), but did not exceed other values from the literature ($e_g = 0.24$; Frisk-Holmberg et al., 1981). It is possible that the ST model underestimates energy expenditure for humans with a

similar FT/ST fiber distribution, but overall the gross energetics of the FT and ST models exhibited a good correspondence with reality.

Whole-body energy expenditure was lowest at 60 rev min⁻¹ for both models (of the specific conditions studied), but the energy expended by the lower limb muscles (Fig. 4) did not necessarily follow the same pattern. In the FT model, energy liberated by the leg muscles decreased from 40 to 100 rev min⁻¹, before increasing at 120 rev min⁻¹. The energy expended by the leg muscles in the ST model was lowest at 60 rev min⁻¹, but was only marginally higher at 80 and 100 rev min⁻¹. For both models, muscle energy expenditure was substantially elevated only at the two extreme cadences. Thus, the “global” view of energy expenditure is a complicated function of the energy expended by the lower limb muscles, plus the contributions made by other parts of the body. While only the legs are actively involved in turning the cranks, energy expenditure from elsewhere in the body may vary with cadence due to variations in circulation and respiration, or changes in muscle activity associated with stabilizing the torso.

The validity of the partitioning of energy between the legs and the rest of the body can be partially assessed using data from Poole et al. (1992) who compared pulmonary and leg oxygen consumption during pedaling at cadences from 60 to 85 rev min⁻¹. Based on their results, leg muscle energy expenditure at 200 W should account for between 75% and 85% of the total. In comparison, energy expended by the model leg muscles represented between 72% and 81% of whole-body energy at the 60 and 80 rev min⁻¹ conditions. Given that the leg muscles do contribute to whole-body energy expenditure during “no-load” pedaling, the energy expended by the residual body mass in the model could be overestimated, particularly at higher cadences where no data are available for comparison. Notably, the energy expenditure from the residual body mass had no direct impact on the optimization results or leg muscle

energy expenditure, as it was constant for any given model/cadence combination.

Lower limb muscle energetics was further analyzed in terms of mechanical efficiency. The mechanical efficiency in this context was defined as work done over a whole activation/relaxation cycle (net work) divided by the total energy liberated (work plus heat), summed over all lower limb muscles. Mechanical efficiency was lower for the FT model than the ST model (Fig. 5), but peaked at a pedaling rate 12 rev min^{-1} higher in the FT model. In contrast, the whole-body energy minima occurred at cadences $17\text{--}20 \text{ rev min}^{-1}$ lower than the efficiency maxima, indicating that the optimal working conditions for the muscles were not coincident with whole-body energy minimization. This underscores the importance of differentiating between the energetics of the lower limb muscles and the whole-body, as they may not exhibit similar energy utilization patterns across conditions.

The current results for muscle mechanical efficiency also provide a contrast with experimental estimates of delta efficiency, which is purported to provide the best in vivo estimate of muscle efficiency during pedaling (Gaesser and Brooks, 1975). Varying trends (increasing, decreasing, or not changing) for delta efficiency across cadences have been reported, which likely reflects the difficulty in estimating efficiency of the underlying muscles from the ergometer load and pulmonary gas exchange (Stainbys et al., 1980). Data in Fig. 5 provide the strongest support for the contention that delta efficiency changes little with cadence (Marsh et al., 2000), at least over the range from 60 to 100 rev min^{-1} . This suggests that muscles operate on the plateau of the efficiency–cadence curve during cycling, with only extreme cadences leading to substantial penalties in efficiency. The current simulation data also provide limited support for reports that delta efficiency increases with cadence (e.g., Böning et al., 1984; Sidossis et al., 1992), but only up to about $70\text{--}90 \text{ rev min}^{-1}$. On the other hand, our data do not support findings that delta efficiency decreases steadily from 40 to 100 rev min^{-1} (Gaesser and Brooks, 1975).

Cadences associated with optimal muscle efficiency ($72\text{--}84 \text{ rev min}^{-1}$) in the models bore a stronger association with typical preferred cadences (approximately 90 rev min^{-1} ; Hagberg et al., 1981; Marsh and Martin, 1997) than did the cadences at which whole-body energy expenditure was minimized ($55\text{--}64 \text{ rev min}^{-1}$), and this may have implications for understanding preferred pedaling rates. If pedaling rate depends on muscle efficiency, then individuals with more FT muscle fibers should have higher preferred cadences (Hagberg et al., 1981). A recent study by Hansen et al. (2002) appears to be the only investigation to address this issue directly. Considered in whole, the data in Hansen et al. (2002) suggest that preferred cadence is not especially sensitive to muscle fiber type distribution, with a tendency

actually in the direction opposite to that predicted above. This may reflect the fact that the preferred cadences in Hansen et al. ($56\text{--}102 \text{ rev min}^{-1}$) corresponded to the plateau region of the efficiency curves noted earlier ($60\text{--}100 \text{ rev min}^{-1}$). In this view, muscle efficiency may act as a factor discouraging the use of cadences below 60 or above 100 rev min^{-1} , but may not exert much influence within that range. Mechanical efficiency is unlikely to be sensed by the cyclist directly, however, various muscle mechanoreceptors and metaboreceptors conceivably could provide cues to adopt, or perhaps avoid, a particular range of cadences (Sparrow and Newell, 1998). Regardless, the discrepancy between our predictions based on fundamental muscle properties, and the contrary results reported by Hansen et al. (2002), can only be reconciled by further research in this area.

5. Conclusion

The present simulation results supported the contention that between-group variations in muscle fiber type distribution contribute significantly to differences in submaximal energetically optimal cadences (Hintzy et al., 1999). However, the whole-body rate of energy expenditure during cycling does not appear to be a valid indicator of the metabolic demands placed on the lower limb muscles across cadences. Mechanical efficiency, which depends on the mechanical and energetic properties of the muscles, peaked at a higher cadence in the FT model than the ST model, but exhibited a rather broad plateau between 60 and 100 rev min^{-1} in both cases. In conclusion, the current simulation results support muscle fiber type distribution as an important determinant of the energetics of submaximal bicycle pedaling.

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