

Muscle Power: The Interaction of Cycle Frequency and Shortening Velocity

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MARTIN, J.C. Muscle power: the interaction of cycle frequency and shortening velocity. *Exerc. Sport Sci. Rev.*, Vol. 35, No. 2, pp. 74–81, 2007. *Force-velocity, force-time, and force-length relations of muscle are typically evaluated with reductionist techniques in which force is measured while the variable of interest is manipulated. However, force produced during voluntary movement arises from complex interaction of these contractile characteristics. Nonetheless, neuromuscular performance for cyclical, work-producing movements can be predicted from the interaction of average muscle shortening velocity and movement frequency.*

Key Words: muscular power, force-velocity, cyclic velocity, excitation, relaxation

INTRODUCTION

Individual contractile properties of skeletal muscle are well known. Primary properties, such as force-velocity, force-time, and force-length relations, are typically investigated using reductionist techniques in which force is measured while the variable of interest is manipulated, and all other factors are controlled. For example, force-velocity relations are usually determined with data collected from protocols that allow the muscle to become fully excited (eliminating force-time effects) before shortening across some predetermined range of length (controlling for force-length properties). Such techniques allow for careful analysis of each property and have formed the foundation for understanding muscular function. However, the highly controlled nature of these protocols limits their direct application to voluntary movement. That is, functional movements may begin before complete excitation (force-time), involve variable muscle shortening velocity and resistive forces (force-velocity), and shorten from one length to another (force-length). In addition, these primary properties are known to be influenced by history-dependent effects, such as force enhancement after stretch (7) and force depression after shortening (8). The influence of these primary and history-dependent effects on muscle force

production and the mechanical characteristics of the movement are schematically presented in Figure 1. Given this complex interaction of factors that influence muscular force during voluntary movement, is it possible to predict performance without extremely sophisticated modeling? Such a predictive capacity would be most useful because it could bridge the gap between reductionist properties and voluntary movements. In this paper, evidence will be presented that, for cyclical, work-producing, muscular actions, performance can be predicted from the interaction of two variables: average muscle shortening velocity and movement frequency. In the initial portion of this paper, basic force-velocity and force-time properties will be reviewed with specific reference to how each influences repetitive muscular contraction. Subsequently, data from human voluntary maximal cycling and cyclic muscle protocols (work loops) will be presented to demonstrate how velocity and time (frequency) interactively influence

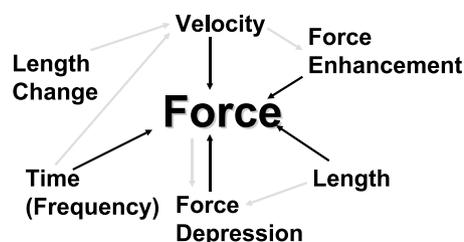


Figure 1. Factors that influence muscle force. Muscular force is primarily influenced by shortening velocity, time (excitation-relaxation), and length. Velocity arises from the time for a contraction (frequency) and the length change within the movement. Velocity influences force directly (force-velocity) and indirectly via force enhancement after stretch. Shortening distance and force determine the work done, which can alter muscle force via force depression after shortening.

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muscular performance during dynamic contractions. Finally, applications for this interaction will be explored, and the similarity of power produced during work loops and maximal human cycling will be examined.

FORCE-VELOCITY

The effects of muscle shortening velocity on muscular force production were first reported by A.V. Hill (9). Representative force- and power-velocity relations are shown in Figure 2 (4). Force decreases with increasing shortening velocity, and the relation is closely approximated by the equation for a hyperbola. Power increases to a maximum at 20% to 35% of maximum shortening velocity and then decreases. These traditional force- and power-velocity relations are determined from protocols that allow the muscle to become fully excited before shortening and, therefore, are not influenced by excitation and relaxation kinetics. Furthermore, although these relations are usually depicted as continuous functions, they are constructed from independent contractions in which the muscle shortens against several discrete loads. In contrast to the discrete velocities and loads used to determine traditional force-velocity properties, most functional movements involve a variable muscle shortening velocity. Typically, velocity will be zero at the start and end of the movement (e.g., maximal and minimal joint extension) and will reach a peak velocity at some intermediate point within the movement. Such a movement often produces a sinusoidal length trajectory, and thus velocity will follow a cosine function. Because of the within-movement variation in velocity, the relation of average muscle force and average shortening velocity may not be immediately obvious.

Caiozzo and Baldwin (4) used traditional force-velocity properties to estimate the work a fully excited muscle might produce during sinusoidal shortening trajectories (Fig. 3). In their theoretical construct of muscle work, the muscle produced isometric force at maximal and minimal length, and force during the shortening phase was a function of velocity. Maximal velocity and, consequently, minimal force occurred at the midpoint of the shortening phase. With this approach, they (4) determined the theoretical

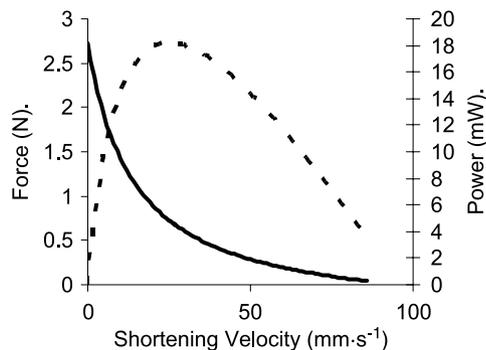


Figure 2. Representative force- and power-velocity relations. Force decreases with an increase in shortening velocity and is well described by the equation for a hyperbola (Hill equation). Power increases to a maximal value (at 26% of maximal shortening velocity in this muscle) and then decreases. Data generated from Hill coefficients for rat plantaris reported by Swoap *et al* (18).

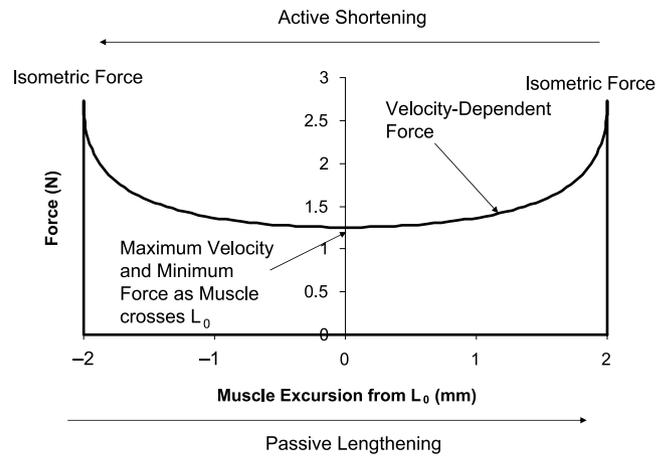


Figure 3. Theoretical work capacity. A theoretical work loop depicts the work a muscle might produce if it could produce fully excited velocity-dependent force throughout the shortening phase and be completely relaxed during lengthening. The sinusoidal length trajectory dictates zero shortening velocity and isometric force at the maximal and minimal lengths. Maximal velocity and minimal force occur at the midpoint of the shortening phase. L_0 refers to optimal muscle length.

work capacity of rat soleus with shortening-lengthening cycles ranging from 0.5 to 4 Hz and excursion amplitudes ranging from 0.5 to 3.5 mm (total excursions, 1–7 mm). From these theoretical data, I calculated values for average force and average velocity (Fig. 4), which indicate that average force was predominately a function of average velocity and exhibited the characteristic hyperbolic force-velocity relation. Thus, traditional force-velocity properties are evident in complex dynamic movements. It is important to note that this measure of theoretical work capacity does not represent actual work production, which would be influenced by other factors, mainly force-time effects or excitation-relaxation kinetics.

CYCLE FREQUENCY AND THE FORCE-TIME RELATION

In addition to the effects of shortening velocity, muscle force is also influenced by time: muscles require time to develop tension and time to relax. Force-time effects may constrain muscular performance during repetitive activities because muscle contractions are often sustained for short periods. For example, cycling is often performed with pedaling rates of 71 to 92 rpm for endurance cycling (11) and up to 155 rpm during maximal sprint cycling (6). At such pedaling rates, each revolution of the cranks must take place in 387 to 845 milliseconds, and the extension and flexion phases must occur within 194 to 423 milliseconds. These time frames likely impose substantial limitations on maximal force production because the time to peak tension in human leg muscles, such as quadriceps femoris (1) and triceps surae (5), have been reported to range from 121 to 400 milliseconds, and half relaxation time has been observed up to 76 milliseconds (5). Consequently, cycle frequency or movement time may limit force production during rapid movements in two ways. First, the time may not be sufficient to allow complete development of maximal muscular force. Second, even if the muscle does reach peak

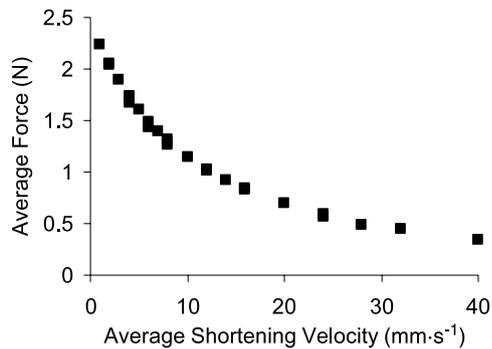


Figure 4. Average force during theoretical work loops. Average force and average velocity calculated from the theoretical work loop data presented by Caiozzo and Baldwin (4). These data show that the characteristic Hill-type force-velocity relation is maintained even when velocity varies sinusoidally within the cycle.

tension within the movement, the reduced force at the onset (excitation) and offset (relaxation) of muscle contraction will reduce average muscle force for the cycle.

Isometric contraction data illustrate the importance of time when considering repetitive muscular contractions (Fig. 5A). These force data were produced by cat gastrocnemius in response to pulse trains (70 Hz) ranging in duration from a single twitch to a train of 32 stimuli (450 milliseconds). When stimulated with a 450-millisecond train, the muscle reached a peak tension of 258 N. The time from the initial pulse until the muscle had returned to 7 N (approximately twice resting tension) was 668 milliseconds, and average active force for that entire excitation-relaxation period was 162 N. When stimulated with a single pulse, peak tension was 47 N, the time to return to 7 N was 101 milliseconds, and average force was 24 N. Intermediate length pulse trains produced intermediate force and duration results.

How do these force-time data apply to repetitive contractions? Many strategies may be used to control repetitive voluntary movements, but one criterion is complete muscle relaxation before a subsequent movement (4). Using this specific strategy, the time required to generate muscle tension and then completely relax would limit the frequency of performing that movement. That is, time to produce tension and relax represents the minimal time required for each contraction, if complete relaxation is the control strategy. In Figure 5B, the average isometric force data are plotted as a function of the reciprocal of total contraction-relaxation time (representing an isometric contraction frequency). When presented in this way, it becomes clear that average muscle force decreases with increasing contraction frequency. These decreases reflect both the failure to reach maximal tension and the reduced force during excitation and relaxation.

WORK LOOPS: A MODEL FOR DYNAMIC MUSCULAR CONTRACTION

Although the data in Figure 5B emphasize the importance of muscle contraction frequency, the results were not influenced by shortening velocity, muscle length, or history-dependent effects that are known to influence force

production during dynamic contractions. Functional movements likely involve complex interactions between these factors (Fig. 1), which make muscular performance difficult to predict from properties determined with reduced preparations. Perhaps because of that complexity, Josephson (10) developed the work-loop technique, which provides a means to study integrated neuromuscular performance during functional dynamic contractions. During a work loop, a muscle is shortened and lengthened (often with a sinusoidal trajectory) by a servomotor and stimulated to produce force while it shortens. Muscular work produced during work-loop protocols has been reported to closely approximate work during *in vivo* movements (16). Force actually produced within a work loop differs from the purely velocity-dependent force in several ways (Fig. 6). Actual force is reduced at the beginning and end of the shortening phase because of incomplete excitation. Depending on the stimulation protocol, some force may be produced before or after shortening, resulting in negative work production. Furthermore, force in the mid-portion of the shortening phase is greater than that predicted by force-velocity properties (17), likely reflecting force enhancement after stretch (8) or tendon compliance. Because several factors besides velocity influence

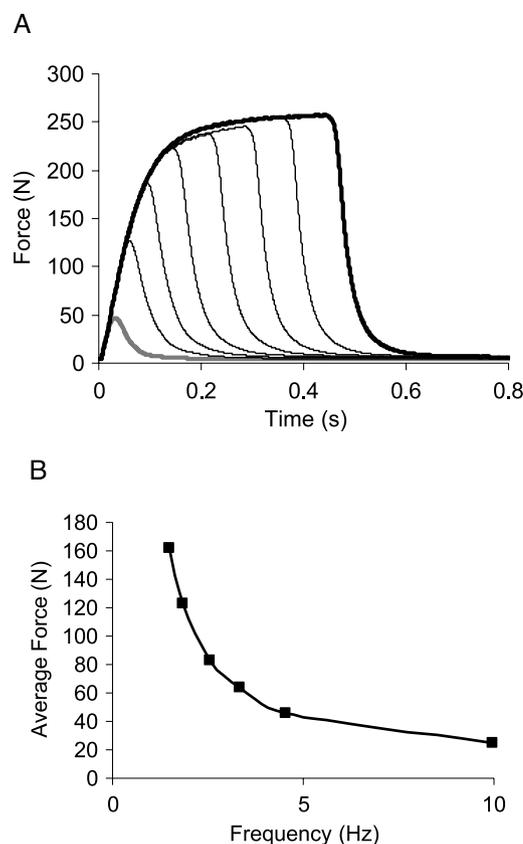


Figure 5. Force-time properties during isometric contractions by cat gastrocnemius. Force-time traces (A) resulting from simulation pulse trains ranging in length from a single pulse (—) to 450-millisecond trains (—). Intermediate durations are all shown as thin black lines (—). Average force (B) produced by each train of stimuli plotted against the reciprocal of the time (frequency) from the initial pulse until the muscle returned to near-resting tension. This representation shows that average force decreased with increasing cycle frequency even for isometric contractions.

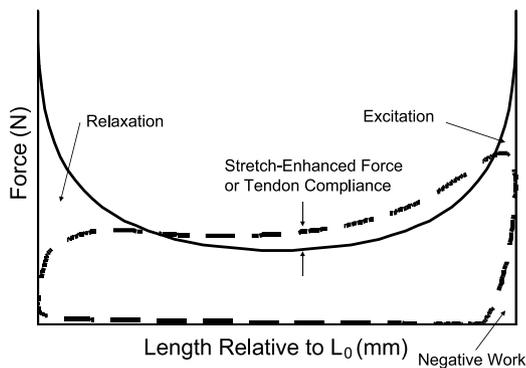


Figure 6. Actual versus theoretical work loops. Force during an actual work loop differs from the theoretical in several ways. Force is reduced during the initial part of the shortening phase because of excitation kinetics (force-time properties). Force is also reduced in the final portion of the shortening phase because the stimulation pulse train must end before minimal length. The muscle continues to produce force as it relaxes, but that force is less than fully excited. The muscle produces some negative work as it lengthens because it was excited before reaching maximum length and because it was not fully relaxed before the lengthening phase. Finally, force was greater than expected during part of the shortening phase, likely reflecting force enhancement after stretch or tendon compliance. L_0 refers to optimal muscle length.

actual work, the ratio of actual work to theoretical work may serve to quantify the effect of the other factors.

Caiozzo and Baldwin (4) calculated theoretical work capacity from force-velocity characteristics and measured actual muscular work performed during work loops. They reported that the ratio of actual muscular work to theoretical work decreased linearly with increased cycle frequency and attributed the decrease to the effects of excitation and relaxation kinetics. Thus, when excitation and relaxation kinetics are subject to history-dependent effects (*i.e.*, enhanced force after stretch and force depression after shortening), they produce a linear reduction in work that is somewhat different from the curvilinear reduction in force in our simplistic isometric analogy (Fig. 5B). Nonetheless, both the isometric and work-loop models illustrate the limiting effect that cycle frequency exerts on neuromuscular function via excitation-relaxation kinetics.

HOW TO SEPARATE FREQUENCY FROM VELOCITY?

For movements of any specified range of motion, average muscle shortening velocity is proportional to cycle frequency. How then can one separate the effects of frequency from those of velocity? One model for separating those effects is to evaluate performance using a range of excursion amplitudes (length change). This might seem a poor choice because muscle force-length properties could influence the work done during a shortening contraction and complicate data interpretation. However, during a repetitive movement, muscle undergoes lengthening before shortening. Consequently, muscle may be subject to stretch-enhanced force production (7) and exhibit a greater plateau region in the force-length relation, and force-length effects will be minimized. Thus, conducting experiments using several cycle frequencies and excursion amplitudes should provide a means to differentiate the effects of velocity from those of

frequency. Several investigators (2–4,18) have used this approach with isolated muscle work loops, and we (12,15) have performed similar experiments using a maximal human cycle ergometry model with a range of crank lengths (excursion lengths) and pedaling rates (cycle frequencies).

CYCLING POWER-VELOCITY RELATIONS

In two previous studies (12,15), we reported maximal cycling power-velocity relations as measured with five ergometer crank lengths ranging from 120 to 220 mm (Fig. 7). The relations between power and pedaling frequency were curvilinear (Fig. 7A), and data for the standard length cranks (170 mm) were typical for the relations reported by others. Although similar in shape, the relationships for each length were shifted along the pedaling frequency axis such that cyclists reached maximal power at lower pedaling frequencies with longer cranks (Fig. 8). The relations between power and pedal speed (Fig. 7B); (pedal speed is an indicator of joint angular velocity and, presumably, shortening velocity of uniaxial muscles (12)) were also similar in shape, but the order was reversed such that cyclists produced maximal power at lower pedal speeds with shorter cranks (Fig. 8). The opposite shifts in these relations suggest that pedaling frequency and pedal speed interactively constrain maximal cycling power. When power was plotted against the product of pedaling frequency and pedal speed (the interaction term, $\text{Hz} \times \text{m}\cdot\text{s}^{-1}$), a construct variable we (12) named *cyclic velocity*, the power produced with all crank lengths, tended to converge—demonstrating that the interaction term governs power across a wide range of conditions. It might seem intuitive that excitation-relaxation kinetics would be important at high pedaling frequency but relatively unimportant at low pedaling frequencies. However, these data show that frequency and velocity interactively constrained power across a very wide range of frequencies including 1 Hz or 60 rpm. Thus, even cycle frequencies that may seem low are influenced by excitation-relaxation kinetics

CYCLIC ANALOG TO FORCE?

The cycling data, previously presented, demonstrate that power is a function of cyclic velocity. When considering various aspects of muscular performance, it is often useful to know force and power. What might be the cyclic analog to the traditional force-velocity relation? To address this question, consider that power is the product of force and velocity. Consequently, traditional force-velocity relations can be determined from power-velocity data simply by dividing power by velocity. Dividing power ($\text{Nm}\cdot\text{s}^{-1}$) by cyclic velocity ($\text{Hz} \times \text{m}\cdot\text{s}^{-1}$) produces a value in units of $\text{N} \times \text{s}$, which is mechanical impulse. Impulse represents the integral of force over time and thus accounts for force and the period over which that force acts. Therefore, impulse may be an appropriate term for describing neuromuscular function during time-dependent actions. Impulse-velocity relations during maximal cycling are shown in Figure 9.

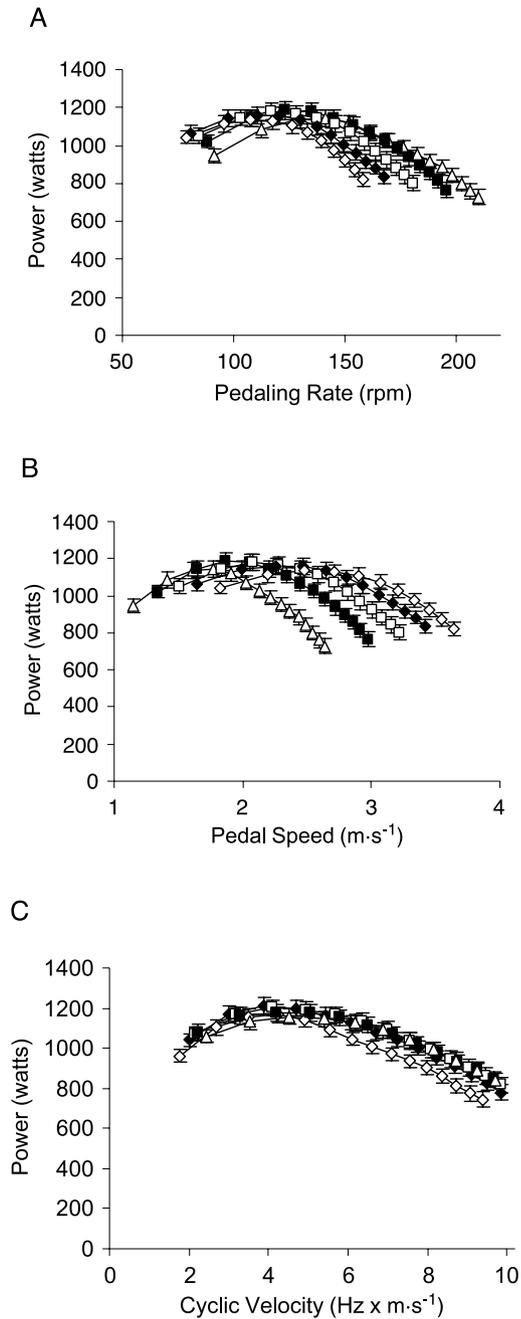


Figure 7. Power-velocity relations during maximal cycling. The relations between power and pedaling rate for five crank lengths (A) were similar in shape but were shifted along the pedaling rate axis such that maximal power occurred at lower pedaling rates with the longer cranks. The relations between power and pedal speed (B) were similar in shape but were shifted along the pedaling speed axis such that maximal power occurred at lower pedaling speed with the shorter cranks. Power for all the crank lengths tended to converge (C) when plotted against the product of cycle frequency and pedal speed ("cyclic velocity"). Crank lengths: Δ 120 mm, \blacksquare 145 mm, \square 170 mm, \blacklozenge 195 mm, \diamond 220 mm. (Reprinted from Martin, J.C., N.A. Brown, F.C. Anderson, and W.W. Spirduso. A governing relationship for repetitive muscular contraction. *J. Biomech.* 33:969-974, 2000. Copyright © 2000 J.C. Martin. Used with permission.)

Impulse decreased with pedaling frequency (Fig. 9A), and the relations were separated such that cyclists produced greater impulses on shorter cranks for any specific pedaling frequency. The overall decreasing relations reflect the

effects of pedaling frequency, which determines excitation-relaxation for all crank lengths, velocity for each length, and the time over which force was produced. The separation of those relations reflects differences due to force-velocity effects. Impulse also decreased with pedal speed (Fig. 9B), and relations were separated such that impulse was greater with longer cranks for any specific pedal speed. That separation was likely because of excitation-relaxation kinetics associated with pedaling frequency. Impulse for all the crank lengths tended to converge to one curve when plotted against cyclic velocity (Fig. 9C), with the exception that the relation for the shortest length (120 mm) differed significantly from the others. Even with that difference, data for all five crank lengths were well represented by a single Hill-type equation ($r^2 > 0.997$) for each individual. The convergence of these relations suggests that "cyclic velocity" accounts for muscle shortening velocity and excitation-relaxation kinetics and thus constrains power and impulse for a broad spectrum of conditions. These data provide compelling evidence that impulse and power are governed by the interaction of cycle frequency and shortening velocity. However, one could argue that they might represent some nuance of voluntary motor control or biomechanics during cycling rather than intrinsic neuromuscular function.

To determine if our cycling results were truly representative of intrinsic neuromuscular function, we (12) made use of work-loop data published by Swoap *et al.* (18). Specifically, we calculated impulse, power, shortening velocity, and cyclic velocity from the data they reported (Fig. 10). Similar to our cycling data, impulse calculated from their work-loop data decreased with increasing cycle frequency but was separated such that impulse was greater for smaller excursions (Fig. 10A). Impulse also decreased with increasing shortening velocity but was separated such that impulse for any specific velocity was greater for longer excursions

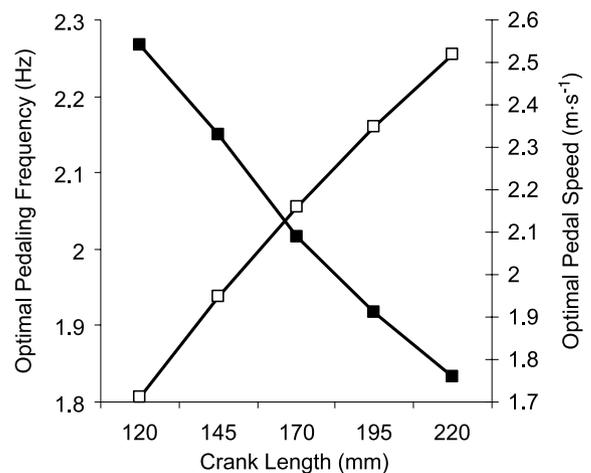


Figure 8. Cycle frequency and pedal speed at maximal power. The cycle frequency at which cyclists reached maximal power decreased with increasing crank length, whereas pedal speed for maximum power increased. (\blacksquare Pedaling frequency, \square Pedal speed). (Reprinted from Martin, J.C., and W.W. Spirduso. Determinants of maximal cycling power: crank length, pedaling rate, and pedal speed. *Eur. J. Appl. Physiol.* 84:413-418, 2001. Copyright © 2001 J.C. Martin. Used with permission.)

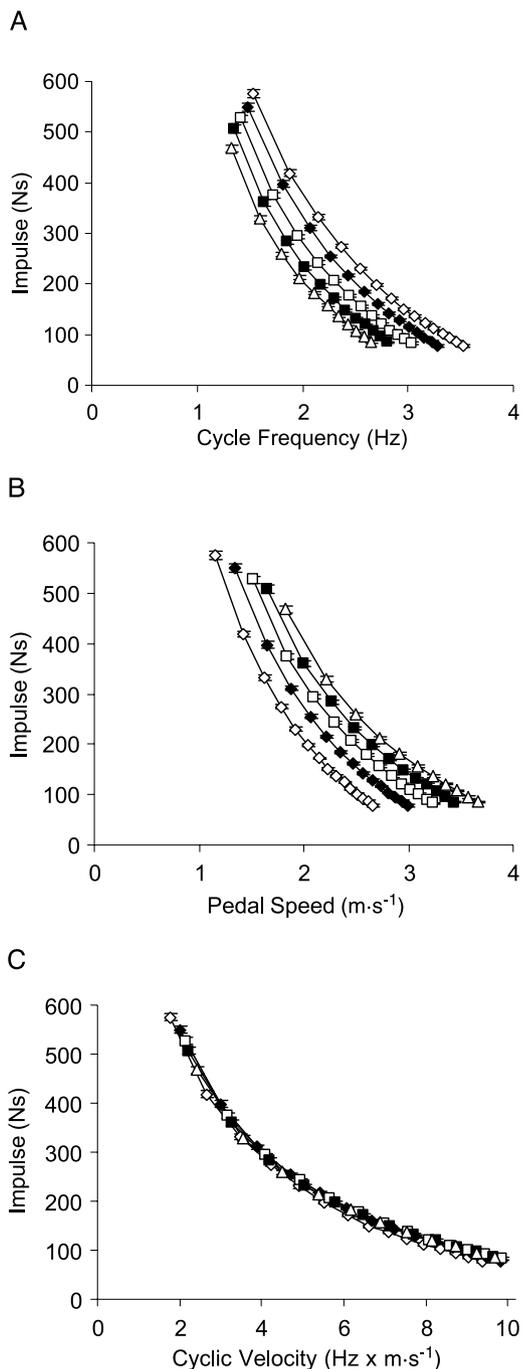


Figure 9. Impulse-velocity relations for maximal cycling. Impulse decreased with pedaling frequency (A) for all crank lengths, and impulse for any specific frequency was greater with shorter cranks. Impulse also decreased with pedal speed (B) for all crank lengths, and impulse for any specific speed was greater with longer cranks. Impulse for all crank lengths decreased similarly with the product of cycle frequency and pedal speed ("cyclic velocity" (C)). Crank lengths: \triangle 120 mm, \blacksquare 145 mm, \square 170 mm, \blacklozenge 195 mm, \diamond 220 mm. (Reprinted from Martin, J.C., N.A. Brown, F.C. Anderson, and W.W. Spirduso. A governing relationship for repetitive muscular contraction. *J. Biomech.* 33:969-974, 2000. Copyright © 2000 J.C. Martin. Used with permission.)

(Fig. 10B). Finally, impulse for all the excursion lengths, except the smallest, decreased similarly with increasing cyclic velocity (Fig. 10C). Data from the smallest excursion length were clearly different from all the other data (similar

to our human cycling data), possibly because of reduced history-dependent effects or tendon compliance (8). Data for all excursion lengths except the smallest were well represented by a single Hill-type equation ($r^2 > 0.987$). These relations from isolated muscle demonstrate that similar relations produced during maximal cycling are representative of basic neuromuscular function and are not an artifact of coordination or biomechanical constraints.

EXCEPTIONS TO THE RULE

Impulse-cyclic velocity relations from work loops and maximal cycling exhibited similar convergence and a similar exception to that convergence. For both models, the shortest excursion (1-mm excursion for the work loops and the 120-mm cranks for cycling) deviated from the other data. The reason for those exceptions remains unknown; however, two explanations seem plausible. First, the small excursions may have been too small to activate history-dependent effects that are known to increase excitation and relaxation rates (3). In that case, cycle frequency would reduce force to a greater extent at these small excursions. Alternatively, impulse and power during the smallest excursions may be greatly influenced by tendon compliance. Specifically, muscles may initially shorten faster than the muscle-tendon unit until the passive force in the tendon reaches equilibrium with the active muscle force. During small excursions, this equilibration process may occupy most or all of the shortening phase. Consequently, muscle force may be reduced because of increased shortening velocity of the muscle fibers relative to the velocity of the muscle-tendon unit.

APPLICATIONS

The relations between power, impulse, and cyclic velocity may be useful in a number of applications. First, these data suggest that maximal power occurs at a unique cyclic velocity but not at a unique shortening velocity. For cycling, the optimal cyclic velocity for all crank lengths was $3.8 \pm 0.1 \text{ H} \times \text{m} \cdot \text{s}^{-1}$ (15). When attempting to maximize power, cycle frequency and shortening velocity must always be considered interactively rather than individually, and the optimal frequency or velocity for a novel crank length can be easily calculated. Furthermore, the relations of impulse and power with cyclic velocity for one excursion length can be used to predict performance for other excursion lengths. This predictive capacity can reduce the need for testing numerous excursion lengths and therefore simplify experimental designs.

Although these relations, demonstrated in healthy non-fatigued humans and animal preparations, are quite convergent, some conditions may arise in which relations for different excursion lengths do not converge. Any condition that alters the force-velocity relation to a greater or lesser extent than it alters excitation-relaxation kinetics could produce nonconvergent relations. If a disease, injury, or fatigue condition altered excitation-relaxation kinetics (e.g.,

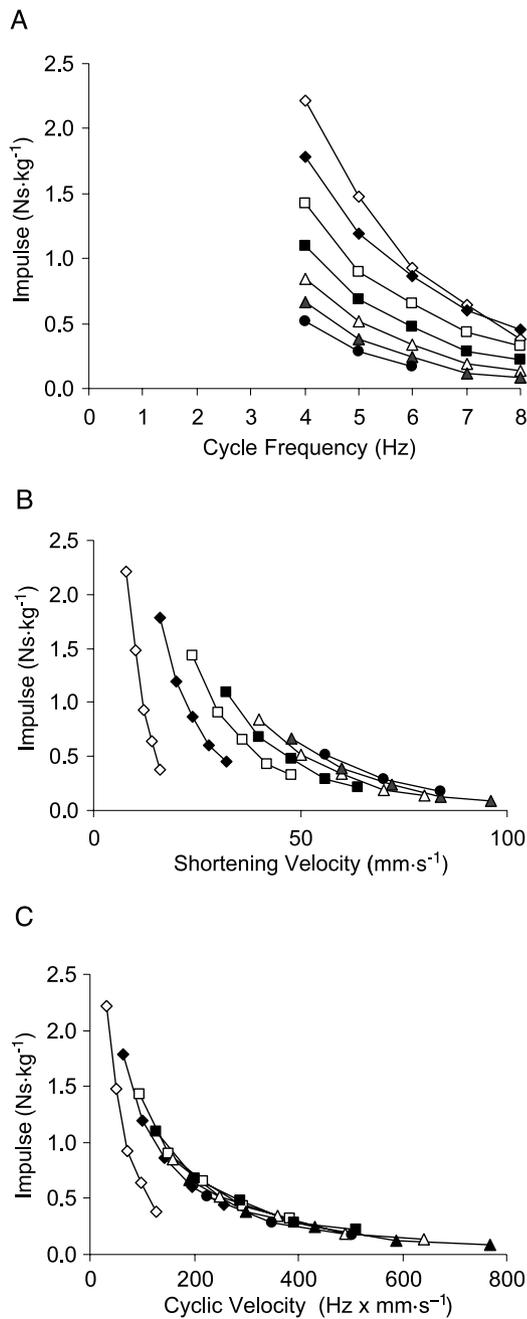


Figure 10. Impulse-velocity relations from rat plantaris work-loop data. Impulse decreased with cycle frequency (A) for all excursion lengths, and impulse for any specific frequency was greater with smaller excursions. Impulse also decreased with shortening velocity (B), and impulse for any specific velocity was greater for greater excursions. Impulse for all excursions (except the smallest) decreased similarly with the product of cycle frequency and shortening velocity ("cyclic velocity" (C)). Excursion amplitudes: \diamond 0.5 mm, \blacklozenge 1.0 mm, \square 1.5 mm, \blacksquare 2.0 mm, \triangle 2.5 mm, \blacktriangle 3.0 mm, \bullet 3.5 mm. (Reprinted from Martin, J.C., N.A. Brown, F.C. Anderson, and W.W. Spirduso. A governing relationship for repetitive muscular contraction. *J. Biomech.* 33:969-974, 2000. Copyright © 2000 J.C. Martin. Used with permission.)

excitation-contraction coupling or calcium ATPase function) to a greater extent than it reduced velocity-dependent force, impulse and power would be improved with greater excursion lengths. This improvement would occur because any specific cyclic velocity arises from a combination of

shortening velocity and cycle frequency. Movements with greater excursion will produce a given cyclic velocity with more shortening velocity and less cycle frequency. Consequently, the effects of excitation-relaxation will be reduced. In contrast, any condition that negatively influenced force-velocity characteristics (e.g., myosin ATPase) would produce less impulse and power for any specific cyclic velocity with greater excursion lengths. In either of these cases, analyzing the degree to which power and impulse did not converge could help to explain the extent to which the excitation-relaxation kinetics differed from normal. These analyses would be more specific to a dynamic task than isometric measures such as time to peak tension or half relaxation time or traditional force-velocity relations.

MAXIMAL POWER: WORK LOOPS VERSUS CYCLING

The characteristically similar relations produced during *in situ* muscle work loops and voluntary maximal cycling suggest that cycling is well represented by work loops. However, the magnitude of those relations was quite different, likely reflecting differences in muscle mass, fiber type, and possibly single muscle versus multi-muscle and multi-joint activity. In an effort to determine just how similar power during cycling and work loops might be, I extracted data from a previous article in which my colleagues and I (13) reported maximal cycling power and muscle volumes determined by magnetic resonance imagery. Normalized power of the 16 subjects, who were younger than 50 yr (the range in which age did not influence normalized power), was $84 \pm 3 \text{ W}\cdot\text{L}^{-1}$ or $79 \pm 3 \text{ W}\cdot\text{kg}^{-1}$, assuming a density of $1.06 \text{ kg}\cdot\text{L}^{-1}$. Although we did not determine muscle fiber type distribution in those individuals, it may be reasonable to assume approximately 50% Types I and II fibers. Comparison of power output with work-loop power is problematic because most of the muscles studied using work loops were predominantly composed of a single fiber type (18). One way to form a direct comparison is to average power output from a mostly Type I and a mostly Type II muscle. Data reported by Swoap *et al.* (18) indicated that rat plantaris (4% Type I) and soleus (95% Type I) produced maximal power outputs of $144 \text{ W}\cdot\text{kg}^{-1}$ and $26 \text{ W}\cdot\text{kg}^{-1}$, respectively. The arithmetic average of those two values suggests that maximal power for a muscle with a fiber type distribution of 50/50 might be approximately $85 \text{ W}\cdot\text{kg}^{-1}$. However, the optimal velocities for plantaris and soleus differ, and an intermediate velocity would be required for maximal power of a mixed muscle. Data for 4-Hz cycling (the smallest used for plantaris and the greatest used for soleus) suggest that a maximal average power of $77 \text{ W}\cdot\text{kg}^{-1}$ would occur at a strain of 4 mm (shortening velocity of $32 \text{ mm}\cdot\text{s}^{-1}$ or a cyclic velocity of $128 \text{ Hz} \times \text{mm}\cdot\text{s}^{-1}$). These human cycling and *in situ* work-loop power data, 79 and $77 \text{ W}\cdot\text{kg}^{-1}$, respectively, are remarkably similar and, although anecdotal, provide additional support for the applicability of work loops to maximal voluntary human activity.

As a final example of the similarity of maximal cycling and work loops, two groups have reported that increasing the

portion of the movement cycle spent shortening increases maximal power. Askew and Marsh (2) reported that power of mouse soleus was 40% greater when the muscle shortened for 75% of the cycle time and lengthened for 25% compared with shortening and lengthening for 50% each. My colleagues and I (14) performed a similar experiment using a maximal cycling model and reported a 4% increase in average power and an 8% increase in instantaneous power when the leg extended for 58% of the cycle. Although our increases in power were smaller than those reported by Askew and Marsh (2), so was our perturbation in pedal trajectory. The perturbation we could impose in that study was limited by our ability to control chain tension on the ergometer. We have since developed techniques that allow greater perturbations in pedal trajectory and have observed that a 70% duty cycle increased power during leg extension by 44%.

SUMMARY

Muscular power and impulse during work-producing actions are interactively constrained by cycle frequency and average muscle shortening velocity. Cycle frequency constrains muscular function via excitation-relaxation kinetics, whereas average shortening velocity represents force-velocity properties. These two factors constrain muscular impulse and power across a very wide range of frequencies and velocities, including low frequencies where excitation-relaxation might not be expected to exert a substantial effect. The interaction of shortening velocity and cycle frequency failed to account for muscular impulse and power at very small excursions, and this may be caused by a lack of history-dependent effects or tendon compliance. Finally, maximal cycling and isolated muscle work loops produce characteristically and quantitatively similar results, suggesting that cycling may serve as a window through which basic neuromuscular function can be observed.

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