# Muscle Activation and Deactivation Dynamics: The Governing Properties in Fast Cyclical Human Movement Performance?

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NEPTUNE, R.R., and S.A. KAUTZ. Muscle activation and deactivation dynamics: the governing properties in fast cyclical human movement performance? *Exerc. Sports Sci. Rev.*, Vol. 29, No. 2, pp. 76-81, 2001. *Repetitive cyclical motion and intrinsic muscle properties each impose constraints on the nervous system to produce well-coordinated movements. We suggest that as cycle frequency increases, activation and deactivation dynamics strongly influence the neural control strategy used and may be the governing muscle property that limits performance. Pedaling and animal studies provide supporting data.* **Keywords:** muscle models, pedaling, simulation, neural control, work-loops, human locomotion

## INTRODUCTION

Human locomotion is characterized by cyclical movements that require muscles to generate mechanical power to overcome external resistive forces (e.g., friction, gravity, and inertia). Muscle power is the product of muscle force and contraction velocity, each of which is influenced by intrinsic muscle properties. The primary intrinsic properties governing muscle force development are the force-length and force-velocity relationships and the kinetics of muscle activation and deactivation. The cyclical nature of locomotion and these intrinsic muscle properties impose several constraints that influence individual muscle function and the coordination of multiple muscles to perform the task. In a stereotyped locomotor movement, the repetitive kinematics dictate the length and velocity trajectories of the muscle-tendon complex, and the intrinsic muscle properties constrain the force that can be developed during the movement. Although the complexity of the interaction between muscle properties and the movement kinematics is well appreciated (7,15), very little is known about the actual in vivo performance of muscles during human locomotion due to the difficulty of performing noninvasive evaluations of muscle force, length, velocity, and activation on human subjects. Thus, much interpretation of neuromuscular function in human movement is based on extrapolating data observed in animal preparations.

Recent studies using work-loop analyses (in vitro or in situ determination of muscle work during locomotor-like cyclical contractions) in animal preparations (5) have highlighted the potential influence that activation and deactivation dynamics can have on the neural control and optimal performance of human movement. In this review, we limit our discussion to the influence of activation and deactivation dynamics during cyclical locomotor tasks and illustrate many of the concepts with supporting data from pedaling studies. Pedaling is an ideal human locomotor task to study gross neuromuscular performance because it is a kinematically constrained repetitive movement that can easily be experimentally manipulated and is amenable to modeling. Pedaling is also analogous to work-loop investigations in that there is a power (shortening) phase during the downstroke and a recovery (lengthening) phase during the upstroke. Although not all muscles are simultaneously lengthening or shortening, comparison with animal studies is justified because the main power-producing muscles fall into this pattern (11).
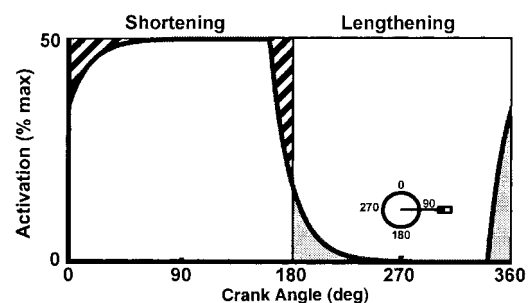
## ACTIVATION AND DEACTIVATION DYNAMICS

Activation and deactivation dynamics are the processes that describe the delay between muscle force development

(i.e., the delay between the neural excitation arriving at the muscle and the muscle developing force) and relaxation (i.e., the delay between the neural excitation ceasing and the muscle force falling to zero) that is a characteristic of the excitation-contraction coupling. These delays in muscle force development and relaxation are due primarily to calcium dynamics and cross-bridge attachment and detachment (15). Most modeling studies of human movement have used Hill-type muscle models in which the activation and deactivation dynamics are represented with first-order differential equations (15) that model the net result of the excitation-contraction coupling, instead of the underlying complex molecular dynamics. The first-order model essentially behaves like a low-pass filter that introduces a delay between the neural excitation and the active state of the muscle. An important characteristic of activation and deactivation dynamics is that the rate of activation is greater than deactivation. In addition, most modeling studies make the simplifying assumption that the activation and deactivation time constants are the same throughout the movement trajectory, even though the rates of activation and deactivation have each been shown in animal preparations to be complex functions of muscle fiber length, velocity, and stimulation frequency (3). It should be noted at this point that the terms *muscle excitation* and *stimulation* are often used interchangeably in the literature when referring to the excitatory signal of the muscle. In modeling studies in which the nervous system is represented, our preference is to refer to the excitatory signal as muscle excitation. When the muscle is externally stimulated, such as during animal experiments or functional electrical stimulation applications, our preference is to refer to the excitatory signal as muscle stimulation. Below, we use these definitions and focus on the results of experimental studies that have tested the influence of activation and deactivation dynamics during locomotor-like movements.

## MUSCLE FUNCTION DURING CYCLICAL CONTRACTIONS

During very slow locomotor tasks, the influence of activation and deactivation dynamics on muscle work production, and therefore the task performance, is minimal (2). However, the time delay involved in activation and deactivation dynamics becomes important in human locomotor tasks that require faster contraction-relaxation cycles (e.g., running, pedaling). During each cycle, a muscle undergoes a shortening phase during which it has potential to generate positive work, followed by a lengthening phase during which it returns to its original length. Assuming an equal duration of muscle shortening and lengthening ($T_s = T_L$) and negligible power required to lengthen the muscle ($P_L = 0$), the theoretical average power over a complete cycle is half of that produced during the shortening phase ($(P_s + P_L)/2 = P_s/2$). However, rarely is this potential fully realized, because the work required to lengthen a muscle is usually not negligible and the work generated during the shortening phase is not maximal because muscle activation and deactivation are not instantaneous processes.

In Figure 1, we present a length-activation relationship of a fictitious muscle undergoing a shortening-lengthening cycle during pedaling to illustrate the consequences of activation and deactivation dynamics. To optimize muscle work production, the muscle excitation must begin during the lengthening phase to account for the delay in activation so that the muscle is generating force at the start of the shortening phase. The extent to which the muscle is not fully active during the shortening phase (Figure 1, crosshatched regions) represents unrealized muscle work. The muscle excitation must also stop before the end of the shortening phase to account for the delay in muscle deactivation to avoid muscle force generation during the lengthening phase. The extent to which the muscle stays active during the lengthening phase (Figure 1, shaded regions) represents negative muscle work that reduces the average power output over the full cycle. Thus, in this simple example, the excitation pattern must balance competing demands to maximize the potential to produce muscle power and work. The excitation must neither begin too early in the lengthening phase, so that excess negative work is generated, nor begin too late, so that too much potential muscle work is unrealized. Likewise, the same tradeoff exists at the end of the excitation pattern, as reducing unrealized positive work results in increasing negative work. As cycle time decreases with faster cycle frequencies, a greater portion of the shortening phase must be dedicated to relaxation to avoid excessive negative muscle work. Thus, there is a trade-off between maximizing positive and minimizing negative muscle work. The likelihood that this trade-off is influential in locomotor tasks has been illustrated by computer simulations of pedaling that show negative muscle work cannot be completely eliminated while satisfying the power output requirement (12). However, note that negative muscle work does not always diminish performance. In some motor tasks (e.g., running), negative muscle work allows the storage of tendon elastic strain energy that can be used effectively in the subsequent shortening phase, and active lengthening before shortening (stretch-shortening cycle) produces force enhancement. In addition, negative muscle work may actually facilitate locomotion through complex biomechanical mechanisms and synergies that allow muscles



**Figure 1.** Hypothetical muscle activation pattern for a fictitious muscle during pedaling using a first-order activation and deactivation model. The muscle excitation is modeled by a block pattern with a magnitude of 50% of maximum and the onset and offset occurring at 342 and 162 degrees, respectively. The muscle is shortening between 0 and 180 degrees. The *crosshatched regions* denote unrealized positive muscle work; the *shaded regions* denote negative muscle work. *Inset*, defines crank angle orientation relative to top-dead-center (crank positioned at 90 degrees).

performing eccentrically to increase energy levels of segments consistent with the task objectives (6,11).

## WORK-LOOP ANALYSES

To further understand the influence of activation and deactivation dynamics on sustainable muscle power across a variety of contractile conditions, studies have analyzed work-loops in animal preparations (5). During a work-loop analysis, an in vitro or in situ muscle undergoes a cyclical length change while being stimulated during the shortening phase to produce positive work. The analysis is usually repeated across a wide range of length trajectories and stimulation patterns (7). Thus, work-loops provide an empirical means to assess the sustainable power output of muscle during repetitive contraction-relaxation cycles that simulate in vivo contractile conditions. When the muscle force is plotted against the corresponding length, the area inside the loop is the net muscle work generated over the cycle, which is equal to the sum of the positive and negative work. Specifically, the net muscle work $W^{mus}$ (J) is computed as:

$$W^{mus} = \int_0^1 F^{mus} \cdot dl \qquad (1)$$

where l (m) is the total muscle length change and $F^{mus}$ (N) is the corresponding muscle force. This equation is equivalent to integration of the instantaneous muscle power over time. An example work-loop is present in Figure 2. Data from one muscle was extracted from a human pedaling simulation where the time histories of the various neuromuscular quantities were precisely known.

Studies have used the work-loop technique to compare theoretical predictions of muscle power based on Hill-type models to power actually measured during work-loops (2,4). Caiozzo and Baldwin (4) performed work-loop analyses of a rat soleus in situ and compared the measured work output with the mechanical work predicted by a theoretical model. The model was based on their measurements of Hill-type force-length-velocity relationships for the muscle but assumed instantaneous activation and deactivation. At low cycle frequencies, the model accurately predicted the muscle output. But as cycle frequency increased, the theoretical model predicted the muscle performance poorly because it overestimated the actual work produced. The discrepancy between the model predictions and the measured output was attributed to muscle activation and deactivation dynamics, which they considered the limiting factor in the mechanical work production. Askew and Marsh (2) performed a similar study by comparing in vitro work-loop measurements of mice soleus muscle with a theoretical model that included not only the measured force-length-velocity relationships but also a model of isometric activation and deactivation dynamics based on the measured force-activation relationship. Again, at low cycle frequencies, the model accurately predicted the in vitro measurements. But as cycle frequency increased, the model with isometric activation dynamics underestimated the amount of muscle work produced. Askew and Marsh (2) inferred from this discrepancy that the rates of activation and deactivation increase with increasing rates of stretch and shortening, respectively. As the rate of muscle stretch increased before shortening, the rate of muscle activation also increased. Similarly, as the rate of muscle shortening increased, the rate of muscle deactivation increased. Thus, the increased rates of muscle activation and deactivation at higher velocities allowed the muscles to generate force for a longer portion of the shortening phase, thus increasing the positive work production, without a corresponding increase in negative work during lengthening (see Figure 1).
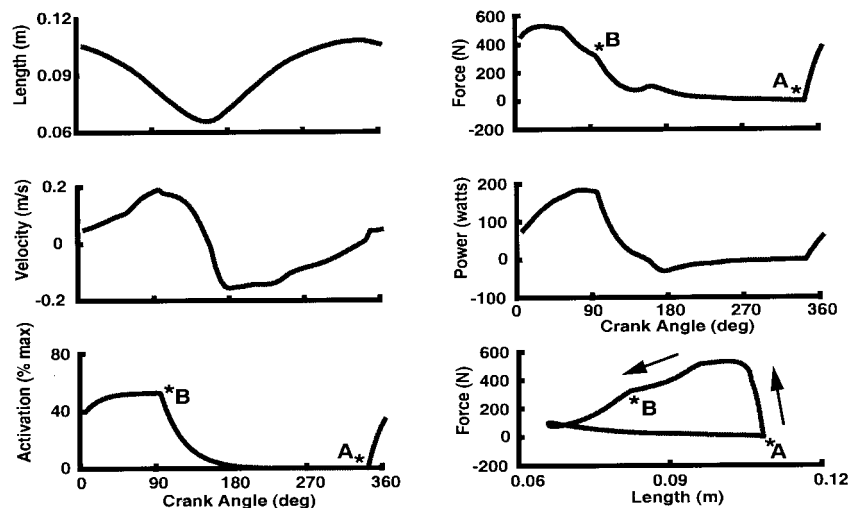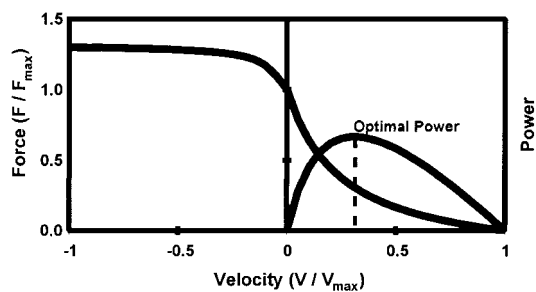


**Figure 2.** Time history of various vasti muscle group neuromuscular quantities during an actual pedaling simulation at 60 rpm (data from Neptune et al. [11]). All quantities were derived from the contractile element (the effect of tendon compliance not shown) in a standard Hill-type muscle model. The first-order activation and deactivation model used time constants of 50 and 65 ms, respectively. The muscle coordination pattern was optimized to reproduce experimentally collected pedaling data from a group of subjects. *A denotes the onset of muscle activity; *B denotes the offset. The force-length curve represents the work-loop over the crank cycle with the area within the loop representing the total muscular work produced. For the contractile element velocity, positive values indicate shortening. Crank angle is 0 degrees at top-dead-center and positive in the clockwise direction.
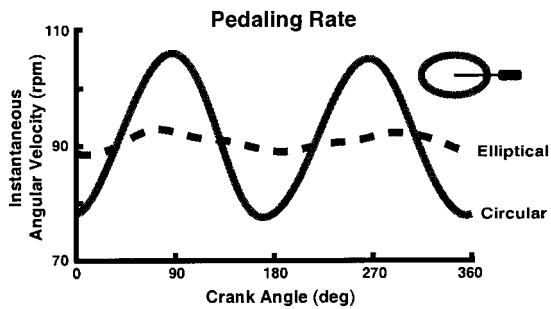
**Figure 3.** The instantaneous crank angular velocity induced by the elliptical (*solid line*) and circular (*dashed line*) chain-rings over the crank cycle (data from Neptune and Herzog [9]). Shape and orientation of the elliptical chain-ring are shown in the *inset*.

These results may explain the results of Neptune and Herzog (9), who investigated how the nervous system adapts to changes in task mechanics by studying cyclists pedaling with an elliptical chain-ring. During steady-state pedaling (i.e., the rear wheel rotating at constant speed), the angular velocity profile of the crank depends on the shape of the chain-ring. A conventional circular chain-ring provides a constant radius from the crank center to the chain driving the rear wheel, which provides a roughly constant crank angular velocity profile. The radius of an elliptical chain-ring, however, varies throughout the crank cycle. Therefore, the constant chain and rear wheel speed during steady-state pedaling requires that the instantaneous angular velocity of the crank varies as a function of the chain-ring radius. Thus, elliptical chain-rings provide an ideal mechanism to change the muscle length trajectory to provide favorable conditions for generating muscle power in a cyclical fashion, very similar in principle to the work-loop studies in animal preparations. The elliptical chain-ring used by Neptune and Herzog (9) changed the kinematics of the crank from a relatively constant angular velocity using a circular chain-ring to a widely varying angular velocity profile (Figure 3). Subjects pedaled at an average rate of 90 rpm with each chain-ring and were required to maintain a constant power output (200 W). The elliptical chain-ring increased the instantaneous crank velocity during the power phase (downstroke) relative to the circular chain-ring (Figure 3). Therefore, it was expected that

*if* the cyclists maintained the same muscle coordination pattern, and hence the same activation levels of those muscles active during the phase of increased velocity (which are the primary power-producing muscles in pedaling [11]), the crank power would increase as the muscles moved up the power-velocity curve. An explicit assumption was that the cyclists were on the ascending limb of the power-velocity curve because optimal power output occurs at much higher pedaling rates (Figure 4) (13,14). However, because the cyclists were required to maintain a constant power output, it was expected that the subjects would have to decrease the muscle activation to offset the increased capacity for muscle power output. But the results showed that there was very little change in the electromyographic timing and magnitude of the major power-producing muscles (e.g., vastus medialis, gluteus maximus), even though these uniarticular muscles were clearly shortening with increased velocity (9). The animal work-loop studies provide one possible explanation for the lack of changes in the electromyogram. During the deactivation of the major power-producing muscles, the non-circular chain-ring increased the muscle fiber velocity relative to the circular chain-ring (9), possibly increasing the rate of muscle deactivation. As a result, the muscle would stop generating force before the end of shortening phase and thus would produce less work.

## INFLUENCE OF ACTIVATION AND DEACTIVATION DYNAMICS ON OPTIMAL PERFORMANCE

Soest and Casius (14) examined maximum power pedaling to identify those contractile properties of skeletal muscle that constrain optimal performance, similar to the goals of work-loop analyses (1,2,4). Using a modeling and simulation-based approach, they optimized the muscle coordination pattern in the simulation to produce maximum power using two models: one that included activation and deactivation dynamics in a Hill-type muscle model, and one that allowed muscles to be activated and deactivated instantaneously. When activation and deactivation dynamics were included, maximum power occurred at 120 rpm, which is similar to the optimal pedaling rate measured experimentally in human subjects (13). Without activation and deactivation dynamics, maximum power occurred at a pedaling rate of 200 rpm and was 60% higher. Their results were consistent with those of Caiozzo and Baldwin (4), who showed in the rat soleus that activation and deactivation time delays alone could reduce muscle power by as much as 60% at higher cycle frequencies, and thus shift the optimal cycle frequency to a lower value. These results suggest that activation and deactivation dynamics, rather than the force-velocity relationship, are the limiting constraint on muscle power and work at high contraction velocities. Thus, performance of a given locomotor task will depend largely on the ability of the nervous system to adapt to the influence of activation and deactivation dynamics, thereby efficiently generating power during the work-loop cycle.



**Figure 4.** Typical force-velocity-power relationship for skeletal muscle. Although the curves are based on data characterizing single muscle fiber behavior, gross muscle behavior and the power output from all working muscles during pedaling are described by similar patterns (13). Optimal power output occurs at a pedaling rate near 120 rpm and diminishes at higher and lower pedaling rates. $F_{max}$ is the maximum isometric force, and $V_{max}$ is the maximum shortening velocity.

## IMPLICATIONS FOR THE NEURAL CONTROL OF HUMAN MOVEMENT

The complex interactions among the task mechanics, intrinsic muscle properties, and performance provide highly nonlinear constraints for the nervous system to generate muscle coordination patterns for a smooth well-coordinated movement. Through learning and experience, it is likely that the nervous system has converged on excitation patterns of individual muscles that accommodate characteristics of the activation and deactivation dynamics and thereby produce efficient or effective performance of cyclical movements. For example, studies in pedaling have shown that muscle coordination (defined by muscle excitation onset and offset timing) systematically phase advances in the crank cycle with increasing pedaling rate, presumably to account for the activation and deactivation dynamics (10).

The interaction between activation and deactivation dynamics and other intrinsic muscle properties can influence preferred muscle coordination strategies. The force-velocity relationship is an intrinsic muscle property that defines the inverse relationship between muscle force and contraction velocity (Figure 4). For a given activation level, the force-velocity relationship defines how the ability of a muscle to generate force decreases with increasing contraction speed. Consequently, there is a defined velocity of muscle shortening for which power production is maximal (Figure 4). Thus, for a given activation level, simply contracting at a faster rate can increase power output if the cyclist is on the ascending limb of the power-velocity relationship. As noted above, maximum power in pedaling has been experimentally measured to occur at pedaling rates near 120 rpm (13). However, during submaximal pedaling, most cyclists prefer pedaling at rates near 90 rpm. Because the average shortening velocity of the major power-producing muscles is presumably slower when pedaling at 90 rpm and because maximum power occurs when the muscles are shortening more rapidly (near 120 rpm), why don't cyclists increase their pedaling rate to move up the power-velocity curve and achieve more power output for the same activation level?

Neptune and Herzog (8) hypothesized that negative muscle work increases at higher pedaling rates as a result of activation and deactivation dynamics and that there is a correlation between negative muscle work and the pedaling rate preferred by cyclists (near 90 rpm). Using a pedal force decomposition technique based on net joint moments, they calculated the negative muscular component of the crank torque over the pedaling cycle. Their results showed that negative muscle work (negative area under crank torque, values shown on Figure 5) significantly increased at higher pedaling rates. At lower pedaling rates (< 90 rpm), virtually no negative muscle work was observed (Figure 5). But at higher pedaling rates (> 90 rpm), significant negative muscle work was generated, and it increased with increasing pedaling rate. These results supported their hypothesis that pedaling rate selection may be strongly influenced by activation and deactivation dynamics. Pedaling at rates greater than 90 rpm would also adversely affect gross muscular efficiency, because any negative muscle work would have to be overcome by additional positive work to maintain a given power output.
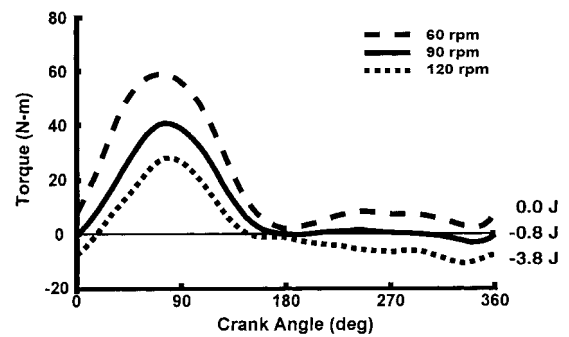


**Figure 5.** Group average muscular crank torque generated over the crank cycle across increasing pedaling rates (data from Neptune and Herzog [8]). As pedaling rate increases, the amount of negative muscular crank torque that hinders crank propulsion increases. Because crank power is a product of crank torque and angular velocity ($P = T \cdot \omega$), there exists a reciprocal relationship between torque and velocity during constant power pedaling. Pedaling at higher rates requires less crank torque to be generated by the cyclist to maintain a given power output. Higher pedaling rates up to 120 rpm take advantage of the force-velocity-power relationship of skeletal muscle, but at pedaling rates beyond 90 rpm, the cyclist's ability to effectively accelerate the crank with the working muscles diminishes and negative muscle work increases.

## IMPLICATIONS FOR EQUIPMENT DESIGN TO IMPROVE PERFORMANCE

Cyclical movements are often characterized by smooth sinusoidal length trajectories (Figure 2, see contractile element length), and in most animal work-loop analyses, sinusoidal length trajectories have been examined . However, alternative length trajectories can provide more optimal conditions to develop mechanical power by taking advantage of intrinsic muscle properties. Askew and Marsh (1) increased the net power output over the cycle by using saw-toothed trajectories that increased the shortening phase relative to the lengthening phase. The increased power was attributed to a more complete activation of the muscle during shortening, in part because of the longer stimulation duration and in part because the increased lengthening velocity increased the rate of activation. In the context of human movement, saw-toothed trajectories are possible in pedaling using noncircular chain-rings that vary the kinematics of the crank arm throughout the cycle, therefore creating more optimal conditions for generating muscle power (9). Thus, based on the animal work-loop studies (1,2,4), an ideal chain-ring design would both increase the shortening phase of the major power-producing muscles and increase the shortening velocity in the time just before lengthening (i.e., increase the rate of deactivation). Increasing the rate of deactivation allows the muscle to be excited for a greater portion of the shortening phase (Figure 1). Then, power could be further enhanced by increasing the rate of lengthening in the time just before shortening to increase the rate of activation. Although such a kinematic trajectory may theoretically increase the power over the cycle compared with a circular chain-ring, the bilateral mechanical constraints associated with conventional coupled pedaling (e.g., increasing the downstroke velocity of the ipsilateral leg will increase the upstroke velocity of the contralateral leg) may make such a chain-ring design difficult to realize. Furthermore, other factors, such as in-

creased joint loading, may cause such a design to be nonoptimal.

## FUTURE RESEARCH

The cyclical motion of locomotor tasks and the intrinsic properties of muscles each impose constraints with which the nervous system must contend to produce a well-coordinated movement. The primary determinants of muscle performance are the force-length-velocity-power relationships and the activation and deactivation dynamics. As cycle frequency increases, activation and deactivation dynamics increase in importance, and they can have a significant influence on performance (2,4,14) and the muscle coordination strategy that is used (8,10). Future research should be directed toward understanding the consequences of the observed complex interactions between muscle fiber length, velocity, and stimulation frequency and the rise and fall of muscle force and integrating these interactions into a comprehensive muscle activation and deactivation dynamics model (e.g., Brown and Loeb [3]).

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