**Optimal workloop energetics of muscle-actuated systems: an impedance view**

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Abstract

Integrative approaches to studying the coupled dynamics of skeletal muscles with their loads while under neural control have focused largely on questions pertaining to the postural and dynamical stability of animals and humans. Prior studies have focused on how the central nervous system actively modulates muscle mechanical impedance to generate and stabilize motion and posture. However, the question of whether muscle impedance properties can be neurally modulated to create favorable mechanical energetics, particularly in the context of periodic tasks, remains open. Through muscle stiffness tuning, we hypothesize that a pair of antagonist muscles acting against a common load may produce significantly more power synergistically than individually when impedance matching conditions are met between muscle and load. Since neurally modulated muscle stiffness contributes to the coupled muscle-load stiffness, we further anticipate that power-optimal oscillation frequencies will occur at frequencies greater than the natural frequency of the load. These hypotheses were evaluated computationally by applying optimal control methods to a bilinear muscle model, and also evaluated through in vitro measurements on frog Plantaris longus muscles acting individually and in pairs upon a mass-spring-damper load. We find a 7-fold increase in mechanical power when antagonist muscles act synergistically compared to individually at a frequency higher than the load natural frequency. These observed behaviors are interpreted in the context of resonance tuning and the engineering notion of impedance matching. These findings suggest that the central nervous system can adopt strategies to harness inherent muscle impedance in relation to external loads to attain favorable mechanical energetics.

Introduction

The capability of skeletal muscles to deliver mechanical power is key in determining the neuromechanical performance envelope of organisms. How fast and how far animals run, fly, swim, or jump is clearly limited by the mechanical power delivered by the muscle-tendon units to skeletal and environmental loads. Therefore, estimating the mechanical energetics of muscles (henceforth simply called energetics) has been of interest in diverse fields such as organismal biomechanics, biomimetic robotics and prosthetics [1–3].

Many factors influence the neuromechanical performance of organisms, including i) the dynamics and mechanical properties of muscle actuators, ii) skeletal mechanics, iii) neural control and iv) influence of loads external to the organism. Integrative approaches have been proposed to capture the interaction of all, or subsets of these factors. For example, the connection between muscle impedance (particularly stiffness) and neural control has been studied in depth with respect to postural and dynamic stability [4,5], locomotory functions [6–9], manipulation [10,11], and other biomechanical tasks [12]. In this work, we adhere to the definition of muscle mechanical impedance as the “static and dynamic relation between muscle force and imposed stretch” [4]. Muscle impedance encompasses muscle stiffness, which is the static relation between muscle force stretch only.

In the context of muscle energetics, most investigations focused on experimentally measuring the power output of individual muscles at a range of frequencies, phases and electrical stimulation parameters, and finding maximal power generating capability of muscles under prescribed motion trajectories. However, the role of muscle-load interaction on output energetics has not been formalized. The central premise of this work is that the mechanical energetics of a muscle-actuated system cannot be determined in a meaningful manner without considering the coupling of muscle properties, load dynamics and neural activation. By considering this coupling explicitly, we arrive at phenomena that cannot be captured using standard workloop testing methodologies, including the opportunity to harness muscle-load interaction in an energetically advantageous manner.

Muscle energetics have been characterized under dynamic conditions, both in vitro [13] and in vivo [9,14,15]. In vitro measurements relied almost invariably on the workloop technique [16]. In this approach, isolated muscles are subjected to predetermined periodic length variations in time (typically sinusoidal, but not always [17]) by means of an external motion source. At a given phase of the imposed oscillation, an electrical stimulus is delivered synchronously, resulting in periodic muscle contractions. A plot of muscle contractile force versus displacement results in a cyclic workloop, with the integrated area within
Author Summary

Movement in organisms is a result of the interplay between biomechanics, neural control, and the influence of external environmental loads. Understanding the interaction between these factors is important not only for scientific reasons but also for engineering robotic systems and prostheses that strive to match biological performance. Muscle mechanical impedance is key in defining the mechanical interaction between muscles and their loads. It is well known that neural activation modulates muscle impedance, particularly stiffness, and that such modulation can be used advantageously to stabilize the posture and motion in organisms. Here, we show computationally and experimentally that stiffness modulation can also be used to enhance the capability of muscle to generate mechanical power, which is key in determining how fast animals can run, fly, swim, or jump.

When muscles are activated optimally in relation to their external loads, they can create resonance conditions at optimal frequencies that significantly enhance their mechanical energetics by up to 7-fold. These findings can be interpreted in the context of the engineering notions of impedance matching and resonance tuning, which are commonly used as guiding principles in the design of diverse power optimal systems, such as communication circuits and robotic systems.

The loop being a measure of the net muscle work done. These and similar measurements have been reproduced in the muscle physiology literature for various muscle groups within various organisms [18–21], and connections between the muscle function and its mechanical energetics have been made [22–24]. While such measurements provide useful energetic connections with muscle function, the experimental conditions do not capture representative in vivo conditions because motion profiles are imposed on single isolated muscles with no muscle-load interactions [25], and without incorporating the effects of antagonist activity. In vivo measurements, on the other hand, capture all of the above effects in principle, but lack the experimental flexibility of varying load conditions in an unambiguous manner.

Capturing the effect of muscle-load interaction on muscle energetics is critical. This interaction can be captured by considering the impedance of the muscles in relation to the impedance of the load. When a group of muscles acts on a common load, as exemplified by an antagonist pair acting on a common load, each muscle forms part of the load borne by the other muscles in its group. Because muscle impedance is activation dependent, neural control can be used to modulate the effective load observed by each muscle by modulating the impedance of the opposing muscles, thereby offering the opportunity to create favorable impedance conditions that maximize power transfer to the external environmental load. This is akin to the notion of impedance matching in engineering systems, where the driving source and the load are “matched” to provide optimal power transfer. In the context of neuromuscular control, impedance matching can enable groups of muscles to work synergistically to provide significantly higher energetics than the sum of individual muscles.

Consequently, in this investigation we studied the influence of muscle-load interaction on muscle workloop energetics both computationally and experimentally. We set up a model problem consisting of a mass-spring-damper system actuated by either a single muscle (Figure 1B), or a pair of symmetric, antagonist muscles (Figure 1D). The input to the system (either neural control or electrical stimulation) can modulate the net force exerted by the two muscles as well as the net impedance. In the context of this problem,
we investigated two hypothesis. Hypothesis 1 states that the power optimal oscillation frequency of a muscle actuated system is greater than the resonance frequency of the load. This is in direct contrast to an impedance-free actuator (such as an ideal electric motor) where the optimal oscillation frequency occurs exactly at the resonance of the load. Hypothesis 2 states that a pair of antagonist muscles can work together to produce more power synergistically than individually by margins that cannot be predicted without explicit incorporation of muscle impedance. We tested these hypotheses both computationally and experimentally. Our computational approach relied on optimal control solutions to the workloop maximization problem, which was based on a mathematical model of the problem. The experimental approach relied on in vivo measurements of workloop energetics of electrically-stimulated, frog muscle acting against emulated mass-spring-damper loads.

Materials and Methods

System Model

To investigate the role of muscle-load interaction and muscle impedance on output energetics, a mathematical model of the problem was developed. This model formed the basis for the ensuing optimization of workloop energetics. We modeled the case of Figure 1D. Note that the case of Figure 1B is a special case of the problem considered with the coefficients of the antagonist muscle set to zero. The key ingredient is a muscle model that captures activation and impedance characteristics of the muscle.

Excitation-contraction dynamics. We assumed the excitation-contraction dynamics had temporal responses that were of the same time scale as that of the oscillatory periods, and consequently cannot be neglected. These dynamics capture the rise and fall of muscle force in time as inputs are applied. They were captured by second order processes with real poles that model calcium diffusion dynamics. We assumed the following model:

\[ \dot{x}_i(t) = p_{x_i} x_i(t) + \beta_i \]

where \( x_i \) is the active state of muscle \( i \), \( \beta_i \) is an intermediate state of \( Ca^{2+} \) diffusion and re-uptake dynamics and \( u_i \) is the electrical stimulus input to muscle \( i \). The parameters \( p_{x_i} \) and \( p_{\beta_i} \) were estimated based on temporal twitch profiles (as detailed in the supporting material Text S1). The parameters used resulted in simulated twitch rise and fall time of 125 msec, and a gain of unity.

Bilinear muscle force model. We assumed that the contractile force exerted by muscle \( i \), \( F_i \), can be approximated by the function

\[ F_i(t) = A_i + B_i x_i(t) + C_i x_i(t) + D_i x_i(t) \]

where \( A_i \) and \( B_i \) are linear in length \( x_i \) and activation \( z_i \). Consequently, the muscle stiffness \( K = \partial F_i / \partial x_i = B_i + D_i z_i \) is linear in activation. The parameters \( A_i, B_i, C_i \) and \( D_i \) were identified based on experimental characterizations that are described in the supporting material Text S1 and illustrated in Figure S1. Similar bilinear models have been used to describe muscle force production in relation to EMG signals in the upper arm \([4,26]\), and also with respect to steady-state force production in electrically stimulated cat soleus muscles \([27]\). In other work \([28]\), we found that for cyclic, bursting contractions, the bilinear model captures 74% of the variance in muscle force production over independent validation sets.

Net muscle force exerted on load. Since the contractile force of each muscle was described with respect to its local coordinates, we used the following transformation:

\[ x_1 = \tilde{x}_1 + x; \quad \dot{x}_1 = \ddot{x} \]

\[ x_2 = \tilde{x}_2 - x; \quad \dot{x}_2 = -\ddot{x} \]

where \( \tilde{x}_1 \) and \( \tilde{x}_2 \) are the nominal lengths of the muscles. Therefore, the net muscle force is:

\[ F_{net} = F_2 - F_1 = (A_2 - B_2(x - \tilde{x}_2) + C_2 z_2 - D_2(x - \tilde{x}_2)z_2) - (A_1 + B_1(x_1 - x) + C_1 z_1 + D_1(x_1 + x)z_1) \]

Load dynamics. The net muscle force excites the mass-spring-damper system and the resulting response is characterized by:

\[ F_{net} = m\ddot{x} + b\dot{x} + kx \]

Interconnected system state equations. From Equations (1), (2), (3), (4) and (5) the dynamics of the interconnected system are written as:

\[ \dot{x} = f(x,u) \]

where the state vector is \( x = [z_1, \beta_1, z_2, \beta_2, x_1, x_2]^T \) and the control input vector is \( u = [u_1, u_2]^T \). The nonlinearity of the system is captured by the bilinear nature of \( F_{net}(x,u) \).

Optimization of Muscle Workloop Energetics

The model of Equation (6) was treated as the basis for our analysis. Since our objective is to analyze optimal muscle workloop energetics, we maximize the average power transfer from the muscles to the load integrated over one periodic cycle. The instantaneous power delivered to the load is given by \( Power(t) = xF_{net} \). The cyclic work done by the muscles on the load is the integral of the power over one complete cycle. Therefore the control inputs, \( u(t) \), that characterize power-optimal oscillations are given by the solution of the following optimization problem:

\[ \max_{u(t)} \int_0^T Power(t)dt = \int_0^T xF_{net}dt \]

subject to \( \dot{x} = f(x,u) \)

\[ u_{min} \leq u(t) \leq u_{max} \]

\[ x(0) = (T) \]
where \( f(x,u) \) is defined in Equation (6) and \( u(t) = [u_1, u_2]^T \) is the control input vector. In this formulation, we assumed that the terminal time \( T \) was given and defined by the objective task. Therefore, to optimize power at oscillations of frequency \( \omega \) [Hz], we set the solution time horizon \( T = 1/\omega \) [sec].

To derive necessary conditions for the optimal solution of Problem (7), we applied the Pontryagin Minimum Principle [29]. We followed the following procedure:

1. Augment the cost function with multipliers for each of the constraints.
2. Define the Lagrangian and Hamiltonian scalar functions.
3. Write the equations governing the dynamics of the optimal multipliers.
4. Define the necessary conditions for optimal control.
5. Solve the resulting 2-point boundary value problem for the optimal state trajectory and the associated multipliers.

Details of this derivation, and the numerical methods employed therein are described as follows. The integrand of the Lagrangian cost function \( L(x,u) \) is given by

\[
L(x,u) = -xF_{\text{net}}
\]

\[
\begin{aligned}
& (A_2 - A_1) - B_2(x - x_1^2) - B_1(x_1^2 + x) + \\
& (C_2x_2 - C_1x_1) - D_2(x - x_2^2)x_2 \\
& - D_1(x_1^2 + x)x_1
\end{aligned}
\]

We augment the dynamical constraints to the cost function, and define the Hamiltonian scalar function

\[
H(x,u) = L(x,u) + \dot{x}^T f(x,u)
\]

From the Pontryagin principle [29], the evolution of the optimal co-state variables at the optimal solutions are governed by:

\[
\dot{\lambda} = -\nabla_x L(x,u) - \nabla_x f(x,u)\dot{\lambda}
\]

The optimal control \( u^* \) is given by

\[
u^* = \arg\min_u H(x,u)
\]

\[
= \arg\min_u L(x,u) + \dot{x}^T f(x,u)
\]

\[
= \arg\min_u \dot{x}^T f(x,u)
\]

where the last equality follows since \( L(x,u) \) is not a function of \( u \) in this particular context. Substituting in Equation (6), we get

\[
u^* = \arg\min_u \left[ \lambda_1(p_{11}x_1 + \beta_1) + \lambda_2(p_{21}x_1 + x_1u_1) + \right.
\]

\[
\lambda_3(p_{22}x_2 + \beta_2) + \lambda_4(p_{22}x_2 + p_{22}u_2) + \lambda_5\dot{x} + \lambda_6 \frac{1}{m} \left( -F_{\text{net}} - b\dot{x} - kx \right)
\]

\[
= \arg\min_u \left[ \lambda_2p_{11}u_1 + \lambda_4p_{22}u_2 \right]
\]

which implies

\[
\Rightarrow u_1^* = \begin{cases} u_{\text{min}} & \text{if } \lambda_2p_{11} > 0 \\ u_{\text{max}} & \text{if } \lambda_2p_{11} < 0 \end{cases}
\]

\[
u_2^* = \begin{cases} u_{\text{min}} & \text{if } \lambda_4p_{22} > 0 \\ u_{\text{max}} & \text{if } \lambda_4p_{22} < 0 \end{cases}
\]

where \( u_{\text{max}} \) and \( u_{\text{min}} \) are upper and lower bounds, respectively, on the control inputs. Depending on the signs of the switching functions \( \lambda_2p_{11} \) and \( \lambda_4p_{22} \), the control \( u_i^* \) assumes either the values \( u_{\text{min}} \) or \( u_{\text{max}} \). This is a bang-bang control solution, and is an expected outcome in such power-optimal (or maximum acceleration) problems [30]. Mathematically, such solutions appear when the Hamiltonian \( H \) is a linear function in the control \( u \), as is the case in this problem. In the absence of limits on the control, the optimization problem would be unbounded, implying that the muscles that can generate unbounded forces will add infinite power to the load. Therefore, for the optimization problem to be mathematically well-posed, upper and lower bounds on the control inputs \( u_1 \) and \( u_2 \) are necessary.

In summary, the first order necessary conditions for power-optimal solutions are given by:

\[
\dot{x} = f(x,u) \tag{8}
\]

\[
\dot{\lambda} = -\nabla_x L(x,u) - \nabla_x f(x,u)\dot{\lambda} \tag{9}
\]

\[
\left\{ \begin{array}{l}
u_1^* = \begin{cases} u_{\text{min}} & \text{if } \lambda_2p_{11} > 0 \\ u_{\text{max}} & \text{if } \lambda_2p_{11} < 0 \end{cases} \\ u_2^* = \begin{cases} u_{\text{min}} & \text{if } \lambda_4p_{22} > 0 \\ u_{\text{max}} & \text{if } \lambda_4p_{22} < 0 \end{cases} \end{array} \right. \tag{10}
\]

with cyclic boundary conditions:

\[
x(t = 0) = x(t = T_f) \tag{11}
\]

\[
\dot{\lambda}(t = 0) = \dot{\lambda}(t = T_f). \tag{12}
\]

Equations (8) and (9) define a two-point boundary value problem (2-point BVP) that is subject to the cyclic boundary conditions (11) and (12) and control constraints (10). This 2-point BVP was solved to give the optimal state trajectory (\( x^* \)), the optimal control inputs \( u^*(t) = (u_1^*(t), u_2^*(t)) \), and the multipliers (\( \lambda \)) associated with the power optimal solution. Methods for solving this problem numerically are detailed in the supporting material Text S1.

**Experimental Methods**

**Ethics statement.** All animals were handled in strict accordance with good animal practice as defined by the relevant national and/or local animal welfare bodies, and all animal work was approved by the MIT Committee on Animal Care (protocol number 0705-051-08).

**Experimental framework.** Experimental investigations played a key verification role in this work in measuring muscle
workloop energetics under the conditions illustrated in Figure 1B and 1D, as well as in generating data sets to identify mathematical muscle models (Equations (1), (2) and (3)) necessary for ensuing optimizations [28]. A full description of the experimental platform and techniques can be found in [25]. For the benefit of the reader, we provide a brief description here.

Explanted muscle experiments were conducted on *Plantaris longus* muscles harvested from adult male *Rana pipiens* (leopard frog). These muscles were chosen primarily for ease of dissection of two contralateral muscles from the same frog, and because their external points provide natural mechanical interfaces to the experimental apparatus (specifically the Achilles tendon and the knee joint). Experiments were performed on single muscle configurations as well as configurations of muscle pairs acting antagonistically as shown in Figures 1B and 1D. These arrangements were achieved by connecting the muscles to load-emulating servo-systems. The servo systems measured the muscle contractile force, and imposed a position trajectory in accordance with the dynamics of the modeled load in real-time, thereby effectively connecting the muscle to mechanical boundary conditions mimicked. In the case of Figure 1D, the interaction of two antagonist muscles acting on a common load was achieved by linking two separate servo-systems in software, i.e. the net direct interaction between the muscle under evaluation, the load (mass-spring-damper in this case). This setup allowed for the two muscles working together on the same load. Here, measurements sets consisted of \( P_\text{a}, P_\text{n}, P_\text{an} \), where \( P_\text{a} \) is the power generated by the agonist muscle only, \( P_\text{n} \) is the power generated by the antagonist muscle only, and \( P_\text{an} \) is the power generated by both muscles working in concert. Similar to the treatment of the data pertaining to Hypothesis 1, measurements were also randomized in their order to factor out the effects of fatigue. The synergistic comparison is captured by the ratio

\[
r = \frac{P_\text{an}}{P_\text{a} + P_\text{n}}
\]

which is computed for each data set. For each muscle pair, measurements were repeated 6 times, with each measurement consisting of the average of 7 oscillatory cycles (with the first cycle discarded as well). We conducted measurements on a load having \( \omega_0 = 2 \text{ Hz} \), with oscillation frequencies set to 3 Hz (3 muscle pairs) and 4 Hz (4 muscle pairs).

In both sets of experiments, the setting of the natural frequency of the load (2–4 Hz) was comparable to frog jumping frequencies (observed at 2 Hz [31]) and frequencies of high muscle power output using the standard workloop technique (observed at 4 Hz [18]). Load stiffness was chosen to be comparable with muscle stiffness (750 N/m to 1500 N/m), and mass and damping ratios (\( \zeta \)) were chosen to limit the amplitude of muscle strain to within experimentally viable ranges.

**Results**

**Optimization Results**

The optimal control problem (Problem (7)) was solved for various values of the time horizon \( T \) that characterized the oscillation frequencies of interest. An example solution is shown in Figure 2 for an oscillation frequency (5 Hz) that is greater than the load resonance frequency (\( \omega_0 = 2 \text{ Hz} \)).

To investigate Hypothesis 1 computationally, successive optimizations similar to those of Figure 2 were conducted as the oscillation frequency was swept across the range of interest, and comparisons between optimal power generated by the bilinear muscle model and the optimal power generated by an impedance free actuator were drawn. As shown in Figure 3A, in the case of the system with \( \omega_0 = 2 \text{ Hz} \), the peak power was generated at \( \omega_{\text{max}} = 2.4 \text{ Hz} \). In Figure 3B, in the case with \( \omega_0 = 4 \text{ Hz} \), the peak power was at \( \omega_{\text{max}} = 4.8 \text{ Hz} \). This result is in direct contrast to the case when the load is driven by impedance-free actuators, where
the optimal driving frequency is exactly equal to the resonance frequency of the load. The increase in optimal stimulation frequency is attributed to the contribution of active muscle stiffness to the net stiffness of the system (shown in the stiffness sub-plots of Figure 2), and thereby tuning the resonance of the combined muscle-load system.

To investigate Hypothesis 2 computationally, we compared the power output of the optimal solutions of the single-muscle case against the optimal solutions of the case of a muscle pair in Figure 4 across the frequency range of interest. The computed power-optimal responses show that synergistic activation of antagonist muscles may produce more cyclic work than individual muscle activation by a factor of more than two (Figure 4B). This is captured by the synergistic ratio $r$, and is in direct contrast to constant impedance actuators where the ratio is exactly two. This model prediction implies that the energetics of individual muscles (obtained by zero-admittance workloop tests) cannot simply be summed to draw conclusions regarding the workloop energetics of the entire system.

**Experimental Workloop Energetics**

Figures 3C and 3D show the results of experimental workloops with single muscles acting on mass-spring-damper loads. To test Hypothesis 1 experimentally, that the peak normalized power output was indeed at $\omega_0 > \omega_n$, measurements were conducted on two load cases with different natural frequencies ($\omega_0 = 2$Hz and $\omega_n = 4$Hz). For both loads, we found that the normalized power measures $\mathcal{P}(\omega_{\text{max}}) > \mathcal{P}(\omega_n)$ and $\mathcal{P}(\omega_{\text{max}}) > \mathcal{P}(\omega_0)$, with $p < 0.01$ for all measurements. We attribute this increase in the optimal oscillation frequency over $\omega_n$ to the stiffness contribution of the muscles. This increase in optimal frequency over $\omega_n$ cannot be achieved via an impedance free force source, and can therefore be directly attributed to the increase in muscle stiffness due to the activation profile over the course of a full cycle.

Figure 5 shows the power output measurements of a pair of antagonist muscles acting synergistically compared to their power output acting individually. When the oscillation frequency was set to 3 Hz, the value of the energetic ratio $r$ was not statistically different from 2. However, when the oscillation frequency was set to 4 Hz, we found $r$ to be $6.96 \pm 1.42$. The ratio $r$ was significantly greater than 2 ($p < 0.01$), showing that the energetics of the muscle pairs are greater than the sum of the energetics attained by individual activation. This is qualitatively compatible with the model predictions plotted in Figure 4 and is in support of Hypothesis 2. This implies the possibility that energetic synergies may be achieved by a muscle-actuated system to enhance their energetic performance at particular frequency ranges.
In the experimental measurements above, the absolute power value of the muscles, normalized by muscle mass, ranged between 17 [W/kg] and 81 [W/kg] at the optimal conditions.

**Discussion**

The role of active and passive muscle impedance, particularly stiffness properties, has been studied intensively in the neuromechanics and motor control literature from the perspective of stability of posture and movement. The main focus of this work is to extend this literature to include the study of muscle mechanical energetics, particularly in the context of periodic motions. We focused on the representative problem of driving a mass-spring-damper by either a single muscle or a pair of antagonist muscles. This setup can be considered as an idealization of a single degree-of-freedom joint.

**Resonance Tuning**

One consequence of explicitly accounting for muscle-load interaction is the increase in the optimal stimulation frequency of the coupled system relative to the natural frequency of the uncoupled

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In the experimental measurements above, the absolute power value of the muscles, normalized by muscle mass, ranged between 17 [W/kg] and 81 [W/kg] at the optimal conditions.
load. This is captured by Figure 3 where the maximal power was generated at a frequency higher than the uncoupled natural frequency of the load, which directly supports Hypothesis 1. This is shown computationally (Figure 3A & 3B) where it is possible to scan the range of oscillation frequencies systematically to search for the frequency of peak power generations, and also experimentally (Figures 3C & 3D) where it is possible to do so only at select frequencies chosen to show the location of peak power. The increase in optimal power generation frequency is not an unexpected result since the stiffness contributions of the muscles should couple in with the overall frequency of the load. What this enables, however, is that resonance conditions can be tuned relative to the desired frequency of oscillation via an appropriate muscle activation pattern.

Taken to the limit of zero load stiffness, we conjecture that this feature potentially enables creating resonance conditions out of non-resonant loads. Consider, as an example, the motion of a swimming fish. The external restoring force on a fish’s body is negligible, therefore the sideways bending dynamics can be considered non-resonant. In the presence of muscle activation, however, significant activation modulate stiffness is added to the system, which can be tuned to the desired oscillatory frequency of the undulating motion. The importance of body bending stiffness in relation to the undulating frequency and speed of swimming fish has been reported in [32,33].

Antagonist Collaboration

Another consequence of the coupling between muscle impedance and load dynamics pertains to energetic synergies that are observed in systems driven by multiple muscle systems. When multiple muscles act jointly on a common load, each muscle contributes to the effective load observed by the other muscles acting on that load. This contribution can be strongly modulated by the neural input to the muscles.

Taking the simplest case of two antagonist muscles acting in parallel on a common load, Figure 5 shows that a pair of muscles can generate more power on a common load than the sum of them acting individually. The margins of collaboration were much higher than those theoretically predicted with impedance-free actuators. For a pair of identical impedance-free actuators, the ratio \( r \) is exactly 2 at all frequencies of oscillation. When one impedance-free actuator is capable of producing more force than the other, the ratio \( r \) ranges between 1 and 2, but never exceeds 2. The maximal value of 2 is achieved if the two muscles provide equal forces, and the minimal value of 1 is approached as the relative contributions of the two muscles vary widely. Ratios greater than 2, as demonstrated in the 4 Hz oscillation case (shown in Figure 5C), and as demonstrated in the maximal values of Figure 4B, are in direct support of Hypothesis 2, and can only be achieved if additional muscle properties are introduced, such as activation dependent impedance.

An Impedance Matching Interpretation

Our findings may be interpreted in the context of the engineering notion of impedance matching. In engineering systems, impedance matching plays an essential role when it is desired to maximize power transfer between two dynamical systems. When a power source is connected in series with a load (in
Figure 5. Experimental arrangements and workloops of agonist and antagonist muscles acting on second-order loads. At certain frequency ranges, the optimal workloop energetics of a pair of antagonist muscles acting in concert is more than the optimal workloop energetics of the muscles acting individually by a factor of $6.96 \pm 1.42$ (representing mean and standard deviation of the averages of 4 muscle pairs). (A) Workloops of agonist muscle acting individually. (B) Workloops of antagonist muscle acting individually. (C) Workloops of muscle pair stimulated out of phase, producing more work on the same load. Asterisks indicate stimulation points (red is for agonist, blue is for antagonist). The first workloop is atypical as the system converges to a steady-state response and is discarded from energetic computations. All workloops have a counter clock-wise direction, indicating positive muscle work, which equals the energy dissipated in the damper. For all cases the natural frequency of the load was $\omega_n = 2$ Hz, $\zeta = 0.3$ and $k = 1500$ N/m. (D) Compiled results for data points similar to A, B and C, with operating frequency = 3 Hz. Data shown across 3 muscle pairs. The workloop energetics of the two muscles working together is not statistically significant from a value of 2 predicted in the theoretical case of...
linear, impedance-free actuators. (E) Compiled results for data points similar to A, B and C, with operating frequency = 4 Hz. Data shown across 4 muscle pairs. The workloop energetics of the two muscles working together significantly greater than 2. The asterisks indicated the p value, with (***) for p < 0.01 and (*) for p < 0.05.

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a Thevenin equivalent connection), maximal power transfer occurs when the internal impedance of the source is equal to the complex conjugate of the load impedance [34]. In a similar manner, neural activation of muscle modulates its stiffness to allow matching of muscle mechanical impedance to that of the load. Therefore, for this source impedance, which is purely reactive, we match the reactive impedance component of the load, certain advantages can be attained. Clearly there are limitations to the value that matches the desired load impedance, energetic tuning, it will decrease the peak-to-peak forces produced by the muscle pair. Beyond a certain break-even point, the peak-to-peak forces will be greatly diminished to the point that impedance matching becomes non-optimal.

Implications on Organismal Motor Control

Research in organismal motor control and biomechanics has reported extensively on the modulation of stiffness in limbs to enhance postural and dynamic stability. Our findings here provide further motivation to hypothesize that the central nervous system may utilize impedance matching as a means to enhance energetics against external loads. Prior studies support the notion that muscle stiffness is modulated to attain resonance tuning, though none have made an explicit energetic connection. Most of these investigations have focused on arm movements. In the context of rhythmic movements, perhaps the clearest evidence was provided in [33], where forearm stiffness was found to increase quadratically with oscillation frequency, and that the stiffness was minimal at the resonance of the load. It was shown that by increasing the oscillation frequency above the load resonance, the arm stiffness increased in a manner that created resonance of the arm-load system. In other studies [36–38], surface EMG measurements in horizontal arm reaching movements have shown that the overall co-contraction levels increase with increasing frequency of oscillation, and that co-activation increases with the square of frequency. Furthermore, in [39], neuromuscular models of the forearm that predict qualitative resonance tuning behavior in rhythmic oscillations were proposed. These arguments have also been extended to the context of of non-rhythmic movements by comparing the average forearm stiffness during reaching tasks with the fundamental frequency content of these movements [40].

The degree to which impedance matching is utilized by organisms specifically for energetic purposes remains to be addressed in future studies. Using antagonist activation of variable impedance actuators can enable the central nervous systems to learn optimal impedances that, when coupled with external loads, can provide higher energetics. Viewed from this perspective, activation dependent muscle impedance may be regarded as a favorable biomechanical property. Furthermore, this postulates that the mechanical energetics of individual muscles cannot be directly summed to estimate the total energetics of a multiple-muscle system.

Supporting Information

Figure S1 Identification of the bilinear model for muscle contractile force. (A) To explore contractile response over a wide range of muscle velocities and positions, oscillatory motions were imposed on the muscles (shown as circles in the position-velocity space). Each circle represents a particular oscillation, with larger circles representing larger amplitudes. Electrical stimulation is triggered at the points indicated by the red asterisks. These were repeated for oscillations at various frequencies, ranging from 1–6 Hz. (B) Typical force trajectories showing modulation of contractile force (as the muscle undergoes oscillations). Experimental measurements shown in black on left, bilinear model estimates shown in blue on right. Red asterisks indicated electrical stimulation trigger points. (C) Contribution of individual model terms to the overall model fit. The bar labeled “All” shows model prediction when all terms from the generalized impedance model

Supporting Information
References


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Author Contributions

Conceived and designed the experiments: WAF HMH. Performed the experiments: WAF. Analyzed the data: WAF. Wrote the paper: WAF HMH.