Unconstrained workloops identify neuro-mechanical resonance as a mechanism for elastic limb behavior

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1 Introduction

Terrestrial biomechanists and roboticists have long accepted that legs behave collectively as a linear compression spring during bouncing gaits like walking, running, and hopping [1-2]. This 'template' for whole limb behavior has led to breakthroughs in understanding both human and animal locomotion, as well as heavily influenced control targets for biomimetic walking robots [3-4]. However, the neurophysiological mechanisms that drive this behavior have remained elusive.

Due to the obvious compliance of the Achilles tendon, many studies have focused on the plantar flexor muscle-tendon complex as a source of elastic limb behavior. Previous studies of human/animal walking, running, and hopping have observed 'tuned' interactions between active muscle, or contractile elements (CE), and series tendon/aponeuroses, or series elastic elements (SEE) [5-6]. Muscle activation is timed in a coordinated manor with body inertial dynamics to produce high forces in active muscle, and store/return large amounts of elastic energy in SEE over a gait cycle. Hopping, in particular, is an excellent experimental model of elastic limb behavior because it is driven primarily at the ankle joint by a single long, compliant muscle-tendon unit (MTU) with a fixed center of rotation and pressure (i.e. biological gearing ratio). This simplifies physiological complexity of movement, and provides an excellent conceptual link to classical in-vitro 'workloop' studies of individual muscle-tendon function.

Workloop studies impose sin-wave like limb/muscle trajectories, and vary phase of muscle activation to explore its role in functional actuation [7]. In bouncing gait, however, limb trajectories are the result of applied patterns of neural stimulation and dynamic environment interactions; not a pre-existing condition to which neural control is applied [8]. In recent years, biologists and engineers have begun developing 'unconstrained' approaches to workloop studies. Robotic systems are used to simulate [9] or coordinate [10] interactions with inertial environments in an unconstrained manor. We adopted a similar approach to explore how MTU material/actuator properties and inertial environment influence neural control patterns yielding 'tuned' interactions.

2 Our Approach

To explore the interplay system material, actuator, and inertial properties in governing tuned muscle-tendon mechanics, we developed a novel bio-robotic framework. Motor controllers were designed to mimic a mass in gravity acting through a fixed mechanical advantage (comparable to the inertial environment of ankle driven hopping), and were rigidly coupled to a biological MTU. If we assume linear behavior from the MTU, classical mechanics says the driving frequency which will yield the most 'tuned' behavior matches that of the passively oscillating system (ω_0), computed as follows:

$$\omega_0 = {}^{l_{in}}/_{l_{out}}\sqrt{{}^{k}/_{M}}$$

Where l_{in} and l_{out} are moment arm lengths, k is passive system stiffness, and M is mass.

Linear behavior is not a given in biological MTU, however. Driving forces are applied internally and are subject to non-linear excitation contraction coupling, non-linear force-length and velocity properties of active muscle, and non-linear passive properties of both muscle and tendon [11]. Additionally, active muscle is subject to history dependent force enhancement and deactivation effects, and tendon is known to dissipate energy over a stretch shorten cycle [7,12]. The goal of this study was to determine how driving frequency relative to ω_0 governs MTU mechanical tuning. We hypothesized that driving

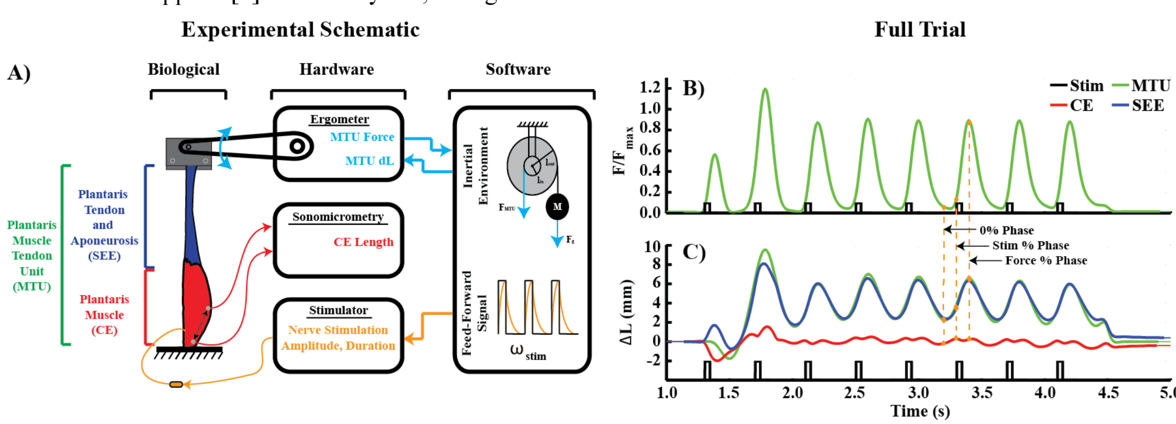

Figure 1: A) Experimental schematic and sample **B)** force and **C)** displacement data from an ω_0 condition used in this study. Note that phasing convention used in this study is annotated between force and length data.

the bio-robotic system at ω_0 would (1) result in maximal peak forces, and (2) minimal fraction of positive work/power from CE. We further predicted (3) emergent (i.e. unconstrained) shifts in frequency-phasing dynamics would facilitate this outcome.

3 Experimental Execution

Experiments presented here use isolated plantaris muscle tendon units from the American bullfrog *Rana Lithobates*. This MTU is an ankle plantar-flexor and has similar morphological and elastic properties to the human triceps-surae Achilles tendon complex. The entire limb was removed, and the plantaris MTU was isolated and mounted into a plexiglass chamber of circulating oxygenated ringers solution. A bipolar stimulating electrode cuff was placed over the intact sciatic nerve to drive muscle contraction. Sonomicrometry crystals were implanted along the line of action of muscle fascicles to independently measure CE displacement. The preparation was rigidly coupled to a feedback controlled servo capable of simultaneously measuring force and controlling position. Motor controllers were designed to mimic a mass in gravity with a fixed gearing ratio (**fig. 1**).

In each preparation (n=5) the MTU was allowed to oscillate passively against the simulated inertial load to measure ω_0 ($\overline{\omega}_0 = 2.34 \pm 0.11$ Hz). Next, the biological MTU was driven for 8 contractions at frequencies from -20%ω_0 to +20%ω_0 in 10% increments in a random order to counteract fatigue effects1. Each contractions had a duty factor of 10% of the cycle period, and consisted of .2ms square wave pulses applied at 100 Hz. The first four contractions allowed the system to reach steady state, and the final four were used in all subsequent analysis.

4 Results/Discussion

For all experimental conditions examined, MTU mechanics stabilized rapidly, and quickly settled into cyclic sin-wave like patterns of mechanics with a net mechanical power of ~0 over a cycle of stimulation (**fig. 1, 2B**).

Hypothesis (1) was somewhat supported by experimental outcomes. Frequency was found to have a significant effect on peak system force (p = 0.032), and the global maximum in peak force occurred for the -10%ω_0 condition (**fig. 2A**). This global maximum was not statistically significantly different from the ω_0 and +10%ω_0 conditions, and significant second order regression fits ($p = 0.037, R^2 = 0.26$) predict a peak in system force for a driving frequency centered *just* below ω_0 (**fig. 2A**).

Maximal fractions of positive work from SEE were observed for a driving frequency of ω_0 in agreement with (2) (**fig. 2C**). This effect was found to be highly statistically significant when subjected to ANOVA testing (p < 0.0001), with the ω_0 condition being significantly different from all conditions except $+10\%\omega_0$. A highly significant regression fit (p < 0.0001, R^2 = 0.71) predicted a maximal fraction of work from SEE for a driving frequency *just* above ω_0.

In general agreement with hypothesis (3), there were emergent shifts in stimulation phasing relative to minimum MTU length that resulted in conditions favorable for elastic energy storage and return (**fig. 2D**). The effect of driving frequency on stimulation phasing was found to be significant (p = 0.004), with the global minimum in phasing occurring for the ω_0 condition (**fig. 2D**). Only the -20%ω_0 condition was found to be significantly different from ω_0 in pairwise tests. Significant regression fits predict a minimum in phasing for a driving frequency *just* above ω_0 ($p = 0.012, R^2 = 0.46$) (**fig. 2D**).

Shifts in phasing were such that stimulation onset was nearly coincident with peak system length/force in the $\pm 20\%\omega_0$ condition, but shifted to preceding peak force/length substantially for intermediate conditions (i.e. $-10\%\omega_0 \rightarrow +10\%\omega_0$) (**fig. 2D**). Having an active CE during system lengthening is favorable for high active force production, subsequent SEE elastic energy storage and return (**fig. 1B,C**), and may substantially increase overall apparent efficiency of compliant MTU function. These results demonstrate that, by proper selection of driving frequency alone, tuned muscle-tendon interactions are an emergent property of system material and inertial properties. No feedback control is required.

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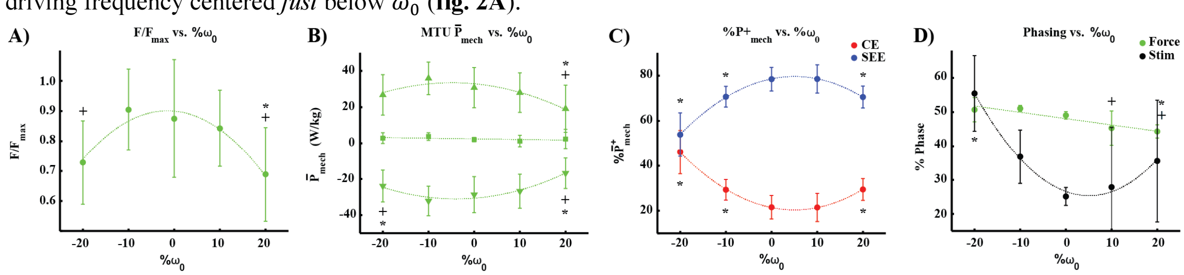

Figure 2: Mean $\pm$ 1 SD for **A)** Peak force, **B)** MTU Average positive (▲), negative (▼), and net (■) power **C)** % of positive power from CE and SEE, and **D)** Phasing of peak force and stim onset relative to minimum MTU length over a cycle of stimulation. A * denotes a significant difference from ω_0, a + denoted significant difference from global max/min if it is not the ω_0 condition.