INTRODUCTION
Series elastic elements (SEE) (e.g., tendon and aponeurosis) are critical for efficient contractions during cyclic, steady locomotion tasks (e.g., walking, hopping, running), as they can store and return significant mechanical energy, reducing mechanical work required by muscle (CE) [1]. In many clinical conditions, the SEE stiffness is altered, becoming either more or less stiff [2]. In addition, the SEE of muscle-tendon units (MTU) tend to get relatively longer when moving from proximal to distal lower-limb joints. The goal of this study was to examine how changes in MTU architecture via altered SEE stiffness impact the ‘tuned’ interaction between CE and SEE during cyclic locomotion. We hypothesized that there would be an optimal, intermediate SEE stiffness that generated high MTU forces, isometric strut-like CE behavior, and facilitated large amounts of elastic energy storage and return in the SEE (i.e., ‘tuned’ MTU dynamics).

METHODS
We employed a MTU model containing a muscle contractile element (CE) with a parallel elastic element (PEE) and a series elastic element (SEE) that acted in opposition to a point mass experiencing constant gravitational forces, simulating MTU dynamics of the lumped ankle plantarflexors during cyclic contractions [3] (Fig. 1). Force was generated in the modeled CE by a Hill-type muscle with classic force-length and –velocity relationships, with stimulation modeled as a square wave pulse with a duty of 10% relative to the cycle period. The PEE and SEE followed non-linear force-displacement relationships taken from recent literature, and the SEE compliance was parametrized by specifying the stiffness, $k_{\text{SEE}}$, in the linear region. To address the role of SEE stiffness on MTU interaction dynamics we compared MTUs with $k_{\text{SEE}}$ in a compliant (=60kN/m), baseline (=180kN/m) and stiff (=540kN/m) setting. Then we performed two simulation protocols on each case: (1) a ‘passive pluck’ of the modeled MTU where the passive components oscillated against the load (i.e. no stimulation, to establish the natural frequency) and (2) a dynamic contraction, where the MTU was actively driven with neural stimulus at the passive natural frequency from baseline condition (=~2.2Hz) and 10% duty factor. Finally, to address the hypothesis, we extracted and compared force, length change and mechanical power dynamics of the MTU, CE and SEE from each simulation case.

RESULTS
The passive resonant frequencies, $\omega_0$, computed based on a period of oscillation from ‘passive plucks’ for $k_{\text{SEE}}/3$, $k_{\text{SEE}}$, and $k_{\text{SEE}}*3$ were 1.64, 2.20, and 2.36 Hz, respectively. Results from the dynamic contractions driven at $\omega_{\text{DRIVE}} = 2.2$Hz and 10% duty (i.e., stimulation period = 450ms; duration=45ms)
demonstrated that in the compliant $k_{\text{SEE}}/3$ condition (i.e., $\sigma_{\text{DRIVE}} > \sigma_0$) (Fig. 2, left), the MTU produced less force, underwent more excursion at lower velocity, and produced less mechanical power than the baseline $k_{\text{SEE}}$ condition (Fig. 2, middle). With a compliant SEE, the CE underwent significant length changes, shortening in the first half of the contraction and performed more mechanical work than baseline. In the stiff $k_{\text{SEE}}*3$ condition (i.e., $\sigma_{\text{DRIVE}} < \sigma_0$) (Fig. 2, right) the MTU produced similar force but at higher rate and with more passive contribution, underwent less excursion at lower velocity and produced less mechanical power than baseline. With a stiff SEE, the CE underwent significant length changes, lengthening in the first half of the contraction and performed more mechanical work than baseline.

CONCLUSIONS
These results strongly support our hypothesis that there is a ‘sweet spot’ in SEE stiffness that leads to ‘tuned’ MTU interaction with high forces and the majority of the MTU mechanical power cycled in elastic tissues. If the SEE is too compliant, the CE undergoes internal shortening, performs significant mechanical work suffers reduced force production force output suffers due to force-length relationship of muscle. If the SEE is too stiff, the CE is passively stretched, and can produces high forces at high rate, but at dangerously long lengths. These results suggest an underlying fundamental principle; that for optimal function, neural drive of an MTU should match its architecture such that it is driven near its passive natural frequency.

REFERENCES

Figure 2. Simulated ankle plantarflexor contraction dynamics for MTUs of varying compliance in steady locomotion cycles. Force, length change, velocity and mechanical power (top to bottom) for MTU (green), CE (red) and SEE (blue) during contraction cycles with $k_{\text{SEE}}$ going from compliant ($k_{\text{SEE}}/3=60kN/m$) to baseline ($k_{\text{SEE}}=180kN/m$) to stiff ($k_{\text{SEE}}=540kN/m$) (left to right). Baseline shows optimal ‘tuning’ for efficient contractions dominated by elastic energy storage and return in SEE.