FROM HOPPING ON LAND TO TREADING IN WATER: UNDERSTANDING LIMITS ON MUSCLE-TENDON PERFORMANCE IN CHANGING ENVIRONMENTS

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INTRODUCTION

Efficient locomotion requires that the neuromuscular system can quickly adapt to internal and external changes [1]. In many terrestrial animals, the external environment in which locomotion occurs may change instantly (*i.e.*, from land to water), resulting in altered locomotion patterns [2]. Determining whether shifts in locomotion behavior are the result of adapted neural commands versus intrinsic mechanics (*e.g.*, shifts in operating point on the FL and FV curves) is difficult to determine *in vivo.*

The goal of this study was to develop a computer model to understand the muscle vs. tendon contributions to locomotion performance when changing from terrestrial to a fluid environment.

We hypothesized that with no change in motor control, in the terrestrial environment muscle (CE) would act as a rigid strut, while in fluids the CE would act as a work producing motor. Additionally, increasing or decreasing the driving frequency in a fluid would increase or decrease the net work produced by the CE, respectively.

METHODS

A mass connected to a muscle-tendon unit (MTU) model containing a contractile element (CE), a parallel elastic element (PEE), and a series elastic element (SEE) was employed (Fig 1A.). The MTU acted through a mechanical advantage to control the motion of a foot. In terrestrial conditions, the mass experienced constant gravitational forces, simulating MTU dynamics of ankle extensors in hopping. In fluid conditions, the mass also experienced a buoyant force, and drag forces at the foot, simulating a treading body in a fluid. Additionally, in the fluid, an antagonist muscle was used to restore the MTU back to longer lengths after a power stroke. Force was generated in the CE by a Hill-type muscle with classic force-length and –velocity relationships and a stimulation modeled as a square wave pulse with a duty of 10% relative to the cycle period. Both the PEE and SEE had non-linear force-displacement relationships taken from the literature. The buoyant force was modeled by: $F_{buoy}=\rho A_x((h/2)-dx)$, where ρ was the density of the fluid, A_x was the surface area of the mass and dx was the change in position of the mass over time. We set Ax to result in a neutrally buoyant case with half the mass above water when dx=0. Drag force experienced by the foot was modeled by: $F_{drag}=-Kv^2$, where v was the velocity of the foot, and K was the lumped drag coefficient (kg/m). Drag only acted when the MTU was shortening, and diminished to zero when the system

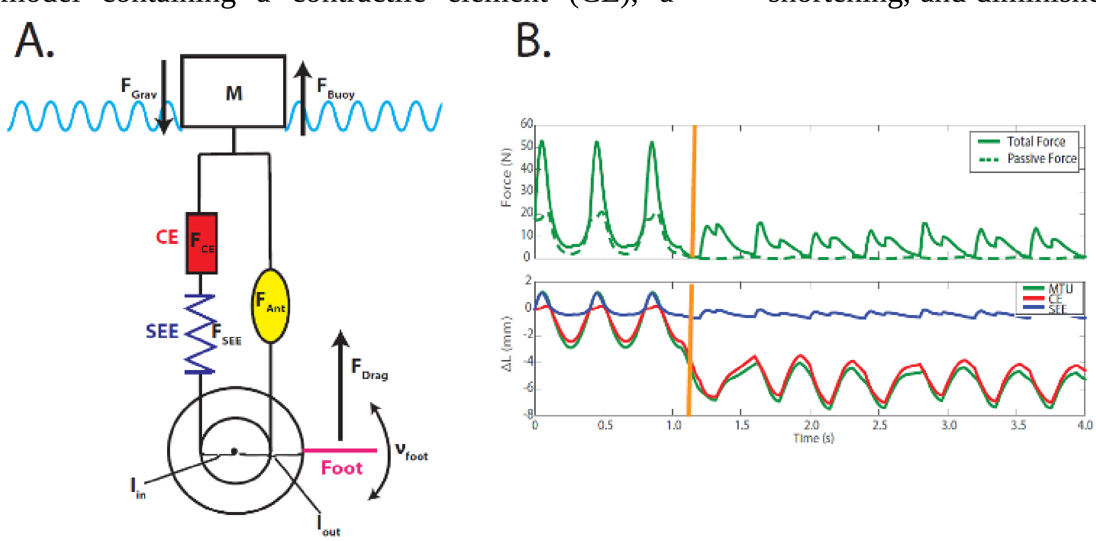

Figure 1. (A) Hopping/Treading Model, (B) Force and length change of the MTU during a terrestrial to fluid transition. A body mass/MTU in gravity operating with a fixed mechanical advantage simulates MTU dynamics during cyclic contractions. In terrestrial states, we set drag coefficient to be sufficiently high to allow hopping like behavior. In fluid, drag coefficient is markedly reduced and the mass experiences a buoyant force to assist the restoration of oscillatory behavior (A). In a transition simulation, the MTU operates at longer lengths and higher passive forces in terrestrial vs. fluid state (*i.e.*, before and after the orange line) (B).

reset due to the action of the antagonist muscle. The action of the antagonist muscle was modeled as an acceleration acting to re-lengthen the MTU, $dV_{MTU}/dt=\alpha*(\Delta L_{MTU})$, where ΔL_{MTU} is the length of the MTU relative to its slack length, and α is a rate constant. To address the role of environmental changes on MTU dynamics, we drove the system at 2.5 Hz, the passive resonant frequency (ω_0) of the system in terrestrial conditions (*i.e.*, gravity only), in both terrestrial and fluid environments. We then shifted the driving frequency to ±20% of ω_0 in fluid to simulate different treading frequencies. To address the hypothesis, we compared the force, length, power dynamics, and work contributions from a steady state contraction in all conditions.

RESULTS

In the terrestrial environment, we observed higher MTU forces with larger passive contribution, longer muscle (CE) operating lengths and higher tendon (SEE) strains than in the fluid (Fig. 1B). In terrestrial simulations, the CE performed isometrically early in the cycle, facilitating large elastic energy cycling to and from the SEE (Fig 2A, B). In fluid simulations, the CE always shortened on stimulation with increasing velocity and force leading to higher power output at higher and higher driving frequencies. higher power outputs (Fig 2A). In fluid, the majority of the MTU work is produced by the CE, rather than the SEE (Fig 2B).

CONCLUSIONS

These results support our hypothesis that (1) muscle (CE) should generate net positive work (*i.e.,* act as a motor) in fluid, and generate zero net work (*i.e.,* act as a strut) while in terrestrial conditions and (2) the net work produced by the MTU can be directly modulated by increasing neural drive in a fluid. Our results demonstrate that spontaneous changes in MTU mechanical function can be mediated directly through changes in the environment dynamics without any adjustment in motor control. Interestingly, in terms of maximizing peak power output of the MTU, driving the system under optimal conditions on land (*i.e.,* at the resonant frequency) when in a fluid results in suboptimal performance. Finding a MTU morphology that can maximize power output in both terrestrial and fluid environments without shifts in motor control may be exceedingly difficult. Future experiments will explore how changes in environmental dynamics influence MTU mechanical function *in vitro* on the benchtop using biological MTUs attached to a 'smart' feedback controlled force ergometer.

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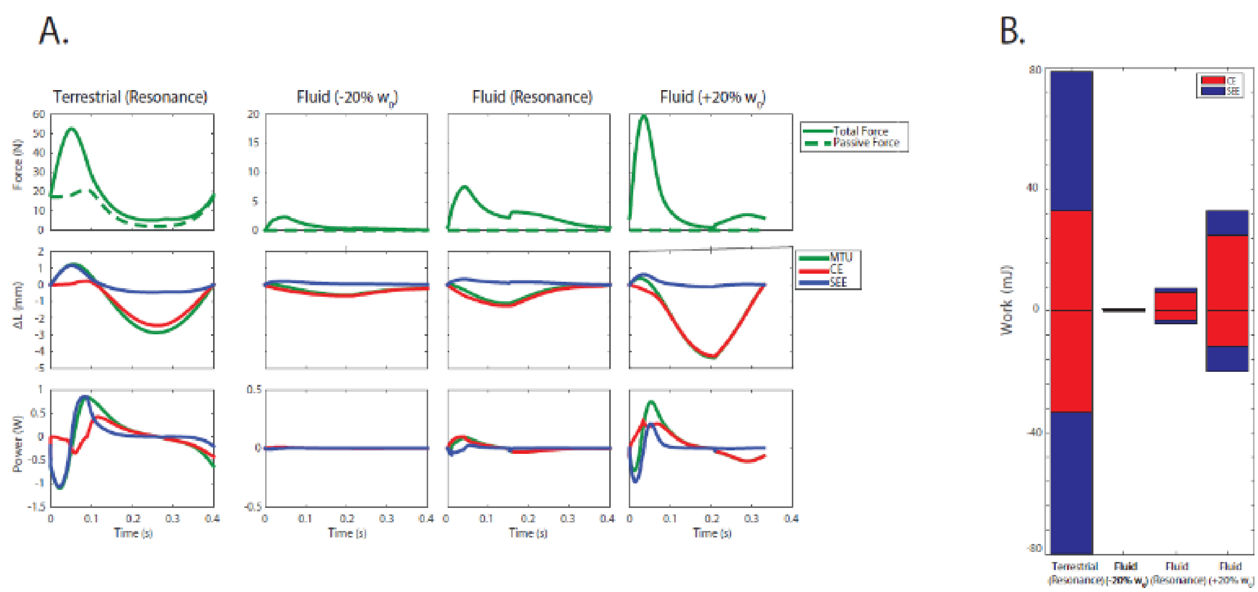

Figure 2. Force, length, and power responses during environmental simulations (A), and work contributions (B). In terrestrial environments, the MTU demonstrates high total and passive forces, isometric behavior during contraction, and increased power output compared to fluid conditions. When driving at increasing frequencies in fluid, the MTU generates greater force while undergoing greater length changes and power production (A). On land there is greater elastic cycling of the SEE, while in a fluid, the majority of the MTU work is produced by the CE, rather than the SEE (B). When driving at increasing frequencies in fluid, CE net work also increases.