A Neuromechanical Model for Examining Viscoelastic Properties and Scaling Effects on Locomotion in a Rat Hindlimb

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Abstract

Mechanical models are useful for understanding the impact of individual components that are intractable for experimental process. This work presents a model for understanding how the viscoelastic (VE) effects of a muscular system impact the control strategies of that system. First, this model has been validated through a number of benchmark processes. Second, this model is tested under a number of different viscoelastic situations. Finally, this model will be used to explore how control systems are implemented to leverage viscoelastic properties in order to take advantage of the available space.

To better understand the how the nervous system utilizes coordinates a complex viscoelastic system, I will:

**Aim 1 - Create and validate a kinematic model of a rat hindlimb with a complete musculature.** A many-muscled model will be developed that includes all major muscles in the rat hindlimb. The mechanics of this model will be validated against existing rodent models by comparing muscle moment arm profiles over joint range of motion. Length- and stimulus-tension parameters for all muscles will be developed.

**Aim 2 – Characterize the viscoelastic parameters for the hindlimb.** Baseline viscoelastic muscle parameters will be developed from experimentally recorded limb motion. These VE properties will be explored to determine how the hindlimb model rejects perturbations and absorbs energy.

**Aim 3 – Investigate neural control strategies for task-specific hindlimb motion.** Muscle activation strategies will be calculated for different limb actions. Neural control systems will be proposed to coordinate the limb in order to create realistic hindlimb motion. Novel tools for developing large-scale synthetic nervous in Animatlab will be created.

Project Motivation

An animal’s nervous and muscular system coordinate activity within an ever-present external environment. The inertial and viscoelastic properties of the body act as a kind of transfer function from neural activation to environmental manipulation (Full and Koditschek 1999). The environment, in turn, can dramatically alter this physiological transfer function as it carries out adaptive behavior (Chiel, Beer, and Sterling 1988; Pfeifer, Lungarella, and Iida 2007). By analyzing the interconnected nature of form and function, it may be possible to better understand how nervous systems allow animals of different sizes to engage in tasks across a range of body sizes and task speeds.

Contemporary biomechanical models often simulate *either* the nervous system or the musculature. These models fail to capture the complex interconnections between the different subsystems that are fundamental to understanding the complete pathway from neural activation to environmental manipulation (Chiel and Beer 1997; Chiel et al. 2009). These models, which serve as the basis for both biological research and robotic design, are most valuable when they provide a holistic interpretation of the animal and the environment it inhabits.

A simulation tool called Animatlab (Cofer et al. 2010) has been used to create neuromechanical models of animals such as a praying mantis (Szczecinski et al. 2017), a rat (Hunt et al. 2015), and a human. Animatlab use uniquely suited to address the interplay of different body systems because it includes both a biomechanical physics environment as well as a neural control system. This allows users to actuate a model in a 3D environment by coordinating neural activations, as well as map reflexive pathways back from the environment into the nervous system.

This work first presents a neuromechanical model of a rat hindlimb with a complete musculature that has been validated against two existing rodent models. The development of baseline parameters for the muscles is discussed. Next, the work discusses plans for exploring the impact of scaling on the limb and studying the consequences that scaling has on muscle activation during swing. Finally, the development of activation strategies is explored in order for the leg to desired tasks and resist perturbations.

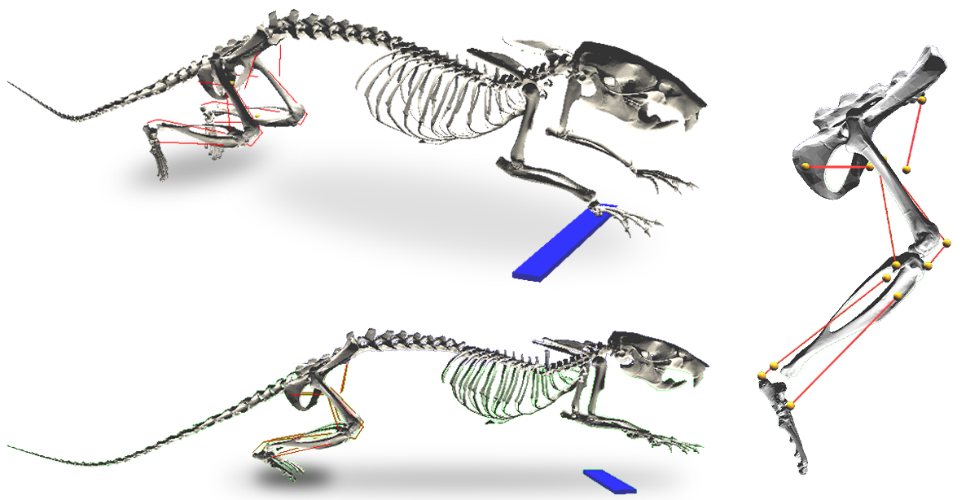
Work that considers both the neural control and the physical system could lay the groundwork for translational research that seeks to model animal activities in robots. In recent years, a growing number of robots have incorporate biological principles into their design in an effort to emulate animal behavior (Webster-Wood et al. 2017; Hunt, Szczecinski, and Quinn 2017; Sharbafi et al. 2016; Schrade et al. 2018; Lakatos et al. 2016). In particular, robots have incorporated muscle-like actuators (Chang et al. 2017) and control systems modeled after spinal cord circuits to coordinate locomotion in legged systems (Beer et al. 1997). Robots offer an exciting research platform for testing hypotheses related to neural control so long as principles related to scaling and task activity are considered.

# Aim 1 - Create and validate a kinematic model of a rat hindlimb with a complete musculature.

## Background

**The goal of this aim is to create a biomechanical model of the rat hindlimb that includes all major muscles, physiologically representative muscle paths, and that is validated against existing rodent hindlimb models.**

This work builds off of a neuromechanical model developed by Dr. Alexander Hunt in completion of a doctoral thesis (Hunt et al. 2014; 2015; Hunt 2016). Hunt's rat model, shown in Figure 1, included a simulated nervous system that coordinated hindlimb muscles to emulate locomotion in a nominal environment using discrete subunits known as central pattern generators (CPGs) (Beer, Chiel, and Gallagher 1999; McCrea and Rybak 2008). This presented a novel method of tuning neural parameters for feedback systems to induce self-supported walking.



**Figure 1** Hunt's rat model. The torso and upper limbs are held stationary above the ground as the hindlimb muscles coordinate locomotion. Red lines indicate muscle paths and yellow markers represent muscle attachment points.

In order to explore how a more generalized nervous system configuration, it is necessary to create a hindlimb model with a complete musculature. Hunt’s model used a reduced muscle set with a flexor-extensor pair at each joint. Muscle pairs were directly mapped to the two halves of a CPG whose oscillation patterns were hand-tuned to recreate walking-like motion by moving the joint.

Hunt’s model makes many simplifications to the rat physiology that hinder our ability to explore interplay between physiology and the environment. In particular, this model fails to capture the complex nature of biarticular muscles (i.e. muscles that span two joints), whose torque profiles are not isolated to individual joints. The first step to enhancing Hunt’s model is to incorporate biarticular muscles and then validate their mechanical advantage against other existing models.

## Sub Aim 1.1: Develop physiological lines of action for all hindlimb muscles

Muscle lines of action in the model are based on anatomical drawings and descriptions from E.C. Greene’s 1955 publication Anatomy of the Rat (Greene 1955). Greene’s work is a primer on rat anatomy that includes hundreds of detailed anatomical drawings and descriptions of rat musculature, nervous system, and circulatory system. Of particular interest to this work are the detailed descriptions of muscle attachment points to bone structures, their relationships to neighboring muscles, and the paths of tendons around joints.



**Figure 2** A neuromechanical model of the rat hindlimb developed in Animatlab with thirty-eight muscles. Colored lines represent muscle lines of action, muscle attachments are shown as small spheres. Colors denote general muscle grouping for visual clarity but do not have a functional significance. Muscle attachment points not directly on a bone surface represent soft tissue attachment.

In simulation, lines of action are created by affixing muscle attachment points onto a 3D rat skeleton. Attachment points (small spheres in Figure 2) remain static in bone-centric reference frame and represent either muscle-bone connections or “via points” to approximate curved muscle paths. Via points were added to muscles such that their lines of action never pass through bone throughout the limb’s range of motion. For muscles that attach to bones along a line of attachment (e.g. the gluteus maximus attaching to the dorsal border of the ilium), a single attachment point was placed approximately halfway along the line of attachment.

Simple hinges were used for the joints with limits set to allow for motion within physiologically plausible regions. Joint centers are stationary relative to the proximal bone and were set such that the distal bone does not collide with other bones throughout the limb’s range of motion.

### Publication

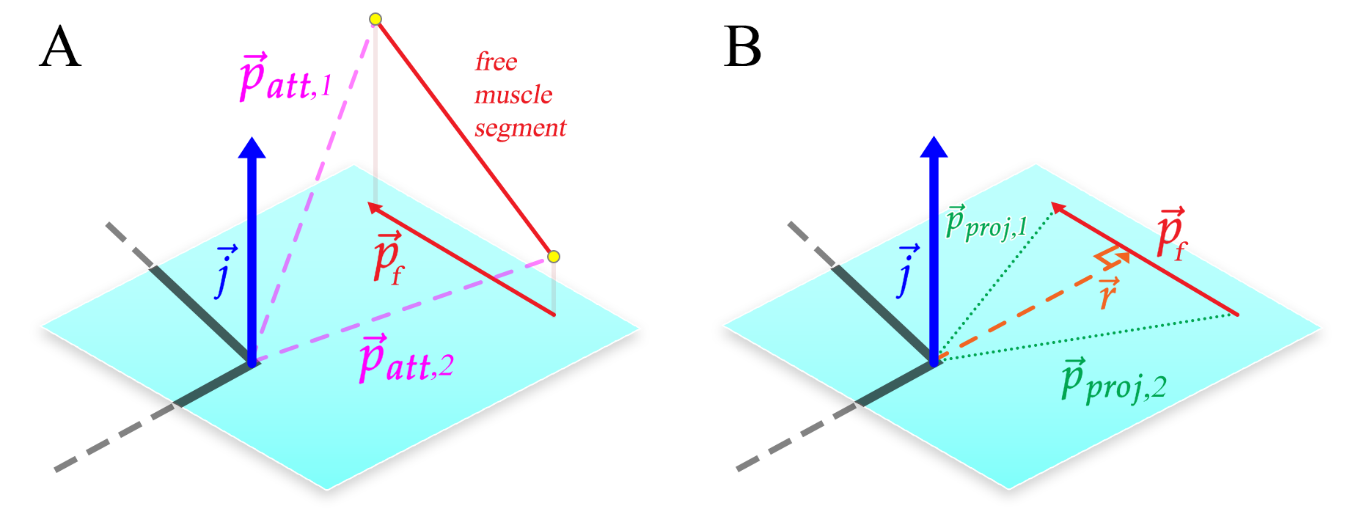
1. Young, F., Hunt, A. J. & Quinn, R. D. A Neuromechanical Rat Model with a Complete Set of Hind Limb Muscles. in Biomimetic and Biohybrid Systems 527–537 (Springer, 2018).

## Sub Aim 1.2: Compare model kinematics to existing rodent models from the literature

With muscle lines of action applied to the model, it was important to validate the model against some existing rodent models (Charles et al. 2016; Johnson et al. 2011). One method for comparing models is to examine muscle moment arm profiles throughout joint ranges of motion. Of particular interest were the mechanical advantages of biarticular muscles throughout motion. WHY?

Moment arms are a representation of the mechanical advantage a muscle has about a joint (Visser et al. 1990; Lee et al. 2008; Williams et al. 2008; Yeo et al. 2011; Charles et al. 2016). Understanding the mechanical advantage of muscles is important for understanding the force contributions a muscle can make throughout motion. Moment arm profiles (the length of a muscle’s moment arm about a joint over its range of motion) are a useful metric whereby a model can be validated against existing hindlimb models.

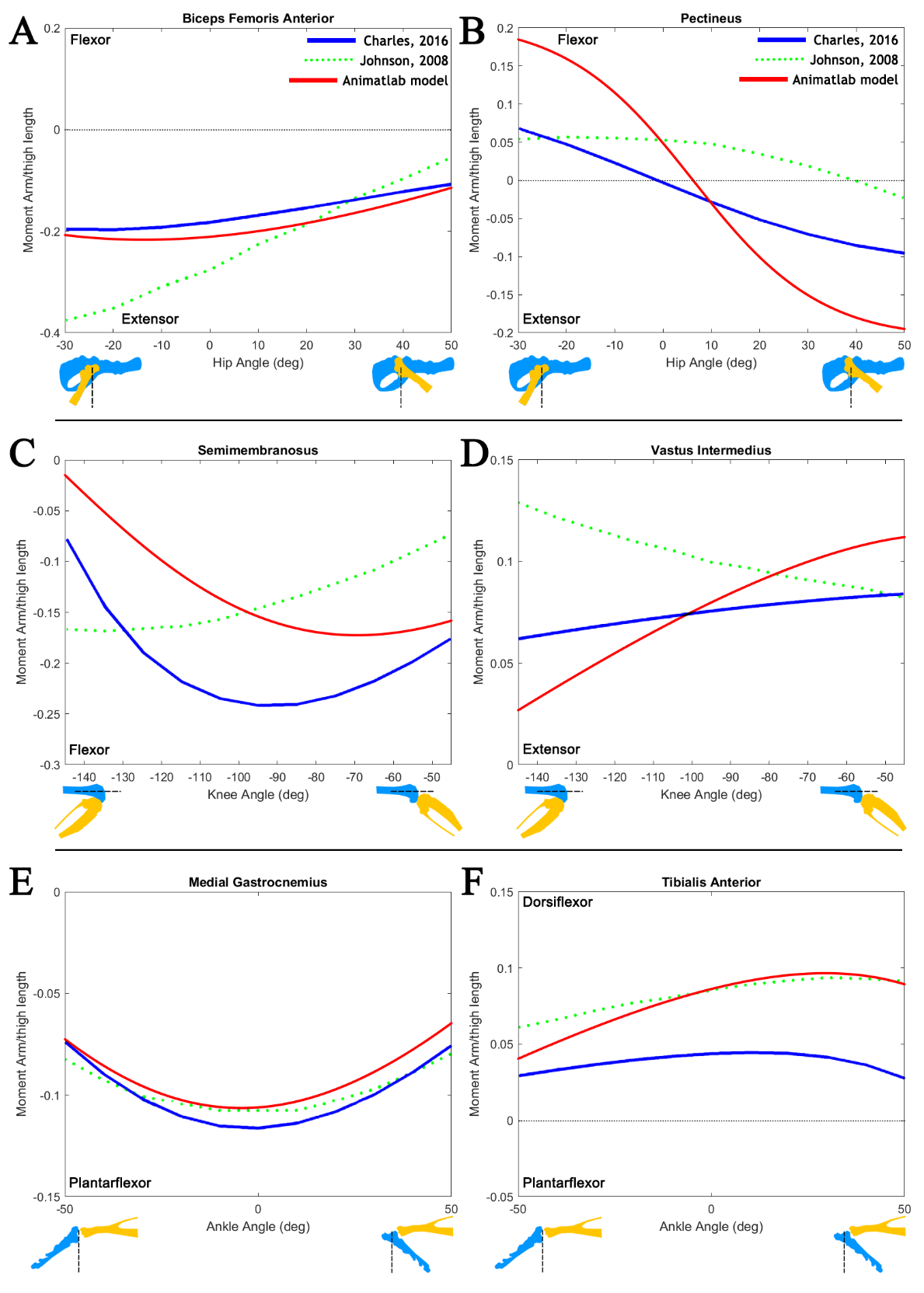
A routine was developed in Matlab (Mathworks, Natick, MA) for calculating moment arm lengths for all muscles when the leg is set to an arbitrary limb configuration. Moment arms were developed using vector analysis, shown in Figure 3, where the muscle is projected onto an orthogonal plane to the joint axis. The moment arm is defined as the perpendicular distance from the joint to a single muscle segment, called the free muscle segment. The free muscle segment represents the part of the muscle that undergoes active length change throughout joint motion. By “driving” the limb with motors placed at the joints, it is possible to develop muscle moment arm profiles over a full joint range of motion.



**Figure 3** The calculation process for muscle moment arms using vector analysis. **A)** The endpoints of the free muscle segment, and ,are projected onto the plane orthogonal to the joint axis, . **B)** The moment arm, , is the length of the perpendicular segment from the joint to the projection of the free muscle segment, .

As seen in Figure 4, a subset of profiles showed comparable magnitude, range, and shape to the Johnson rat model and the Charles mouse model. In general, the model showed strong agreement to the results from Charles but differed notably from the Johnson model for the pectineus, semimembranosus, and vastus intermedius (Figure 4 B-D). The exact reasons for this are difficult to determine because the process for Johnson’s moment arm calculation is not well defined.

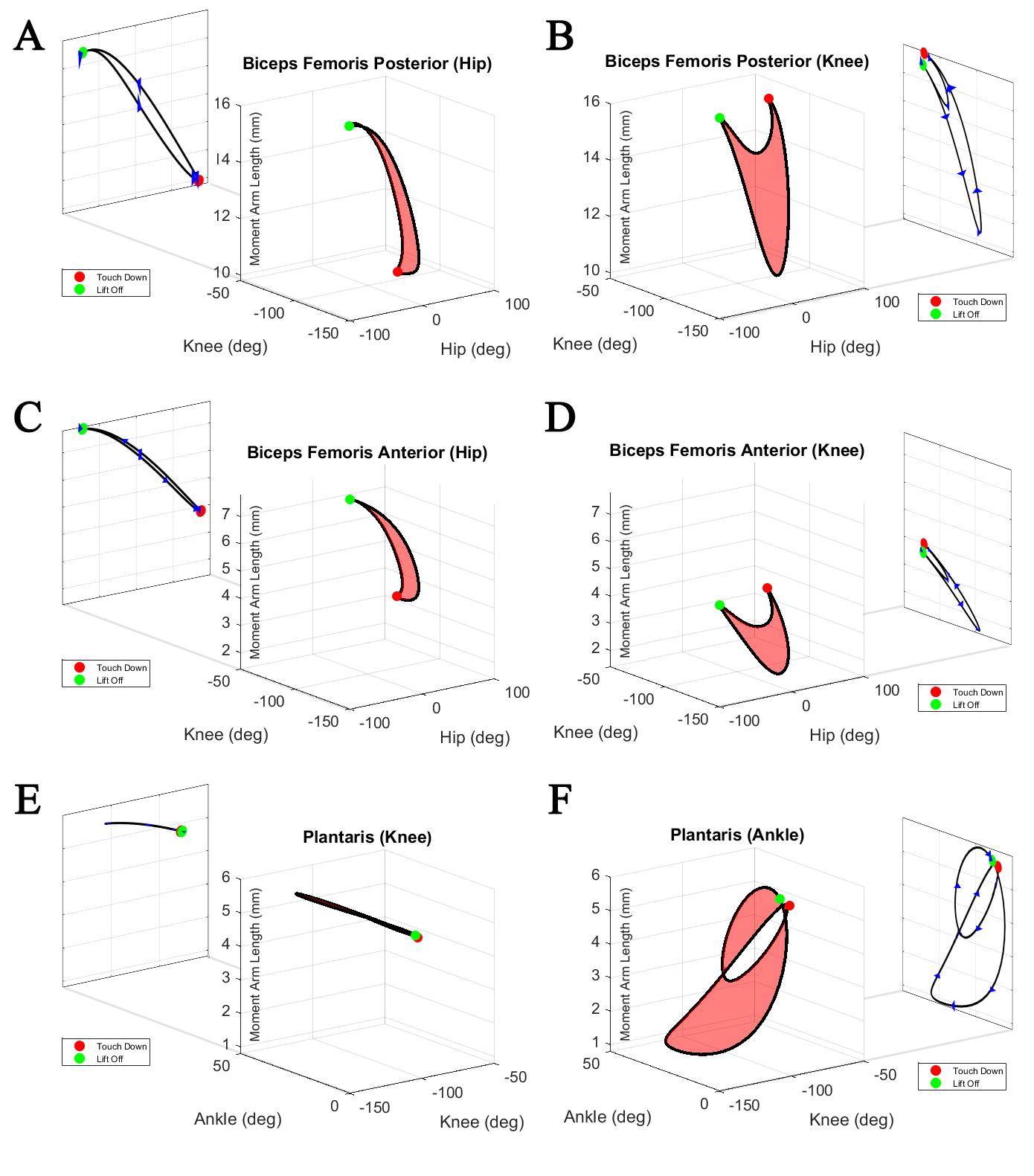
One reason for considering the validity of the Charles moment arms over the Johnson moment arms is that general trends in select muscles make more physiological sense for the former. For example, Johnson’s model indicates that the pectineus is primarily a flexor for the majority of hip motion when it’s been shown to switch from a flexor to an extensor around the middle range of the hip motion.



**Figure 4** Moment arm profiles for select muscles in comparison to two existing rodent models. Moment arm profiles show most similarities with the Charles mouse model. It is difficult to determine the cause of deviations from Johnson’s model since the method used to calculate them is not well defined. Some trends in the mechanical advantage (e.g. pectineus) make more sense for Charles than Johnson.

Of particular focus in this work were the profiles of biarticular muscles about their spanned joints. Biarticular muscles are important to include in the model as shown in Figure 5. The mechanical advantage of biarticular muscles change throughout motion. Characterizing these 3D profiles shows how the different these profiles are.

In addition to calculating moment arm profiles, a sensitivity analysis was conducted to examine the impact of muscle attachment point placement on sagittal plane moment arm profiles. The sensitivity analysis showed that moment arm profiles were robust and maintained their shape across limb configurations even when muscle attachments were shifted independently.



**Figure 5** Moment arm profiles for the biceps femoris posterior across the hip and the knee. **A)** Across the hip, the BFP has different has a small mechanical advantage at touch down but a large advantage at lift off. **B)** For the knee, the BFP has a similar mechanical advantage at touch down and lift off.

### Publications

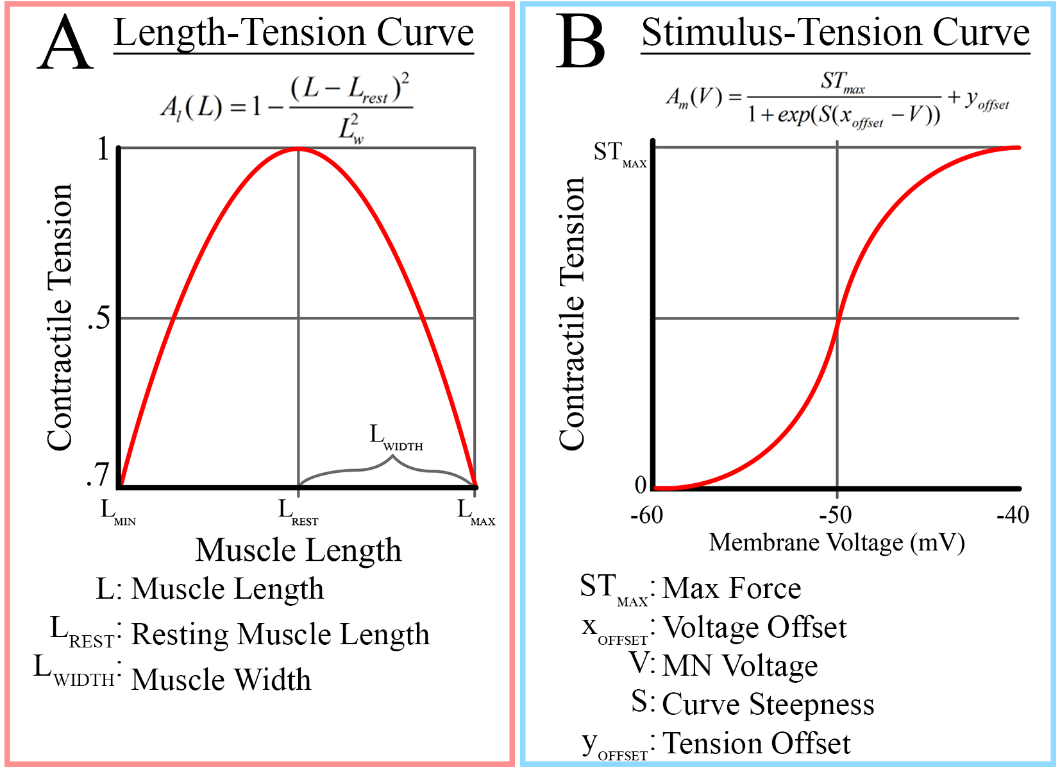
1. Young, F., Rode, C., Hunt, A. & Quinn, R. Analyzing Moment Arm Profiles in a Full-Muscle Rat Hindlimb Model. Biomimetics 4, 10 (2019).

# Aim 2 – Characterize the viscoelastic parameters for the hindlimb.

Recent work shows that animals at different sizes utilize control strategies that are unique to their length scale (Vogel 2005). For example, by measuring muscle activation levels in a stick bug, we can see that the animal engages muscles throughout the entirety of swing to bring the leg forward. In contrast, measurements in horses show that there is very little neural control in early swing phase, presumably because the horse uses inertia to “throw” its leg forward. These two different control strategies illustrate the broader concept that animal nervous systems have adapted to navigating the world differently depending on the size of the animal. **The goal of this aim is to model the viscoelastic properties of the rat hindlimb and compare how passive force distribution changes with respect to scale.**

## Sub Aim 2.1: Develop length-activation parameters for all muscles

The first steps toward this goal are to develop baseline parameters for all muscles. The development of muscle parameters falls into two categories: length-activation profile parameters and viscoelastic parameters. Two tension relationship curves dictate the force generating capabilities of the linear Hill (Hill Archibald Vivian 1938) model: the length-tension (LT) curve and the stimulus-tension (ST) curve. These curves are represented by the terms Al and Am in Equation . The LT-curve relates a muscle’s force-generating capabilities at various isometric lengths while the ST-curve relates the membrane potential to force output.



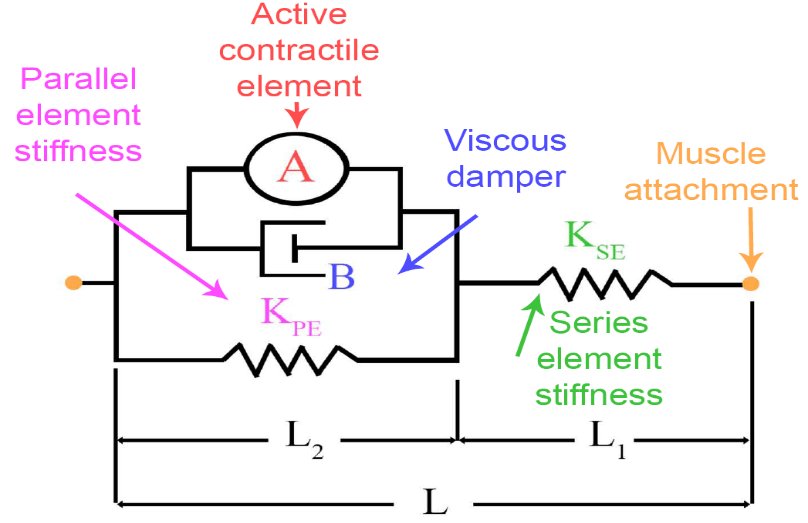
**Figure 6 A)** The length-tension curve defines the ability of muscle activation to generate tension at different muscle lengths. The output of this curve ranges from [0,1]. **B)** The stimulus-tension curve relates motoneuron activation to the tension in the muscle. The output range of this curve is [0, STmax].

The LT-curve (Figure 6A) relates the maximal tension generating capability of muscle at different lengths, where the muscle is capable of generating the maximum possible force at its resting potential. The resting length for muscles is determined by moving the leg through its full range of motion (i.e. from Lmin to Lmax) and finding the midpoint between these values. Based on assumptions from Zajac (Zajac 1989), the muscle width is set such that at the length extremes the muscle is capable of generating 70% of its maximum tension.

The ST-curve (Figure 6B) relates the motoneuron activation to muscle tension. No tension is generated at a resting potential of -60mV, while at full activation (-40mV) the muscle generates a maximal contractile force, STmax. STmax is set such that at steady state, the activation term is capable of generating the maximum tension from the literature, Fmax. Calculating the value of STmax is described in the supplementary material.

Sub Aim 2.2: Calculate baseline viscoelastic parameters for all muscles

Animatlab includes a two-compartment, linear Hill muscle model (Figure 7) with an elastic spring element (KSE) representing connective tissue in parallel with a damping element (B), parallel spring element (KPE), and a contractile element (A). Physiological parameters for rat hindlimb muscles exist in the literature (Johnson et al. 2011; Eng et al. 2008) but efforts to fit these values to the model could not converge to stable solutions.



**Figure 7** The linear Hill muscle model implemented in Animatlab. The force generating component, A, is composed of a length-tension and stimulus-tension term. Circular ends represent muscle attachment points connected to bone meshes.

The nonlinear tension of the Hill model has been formalized (Shadmehr and Arbib 1992) as,

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where T is muscle tension, dt is the physics timestep,  is series element stiffness,  is parallel element stiffness, L is muscle length, B is the muscle damping, is a dimensionless tension-length percentage, and  is muscle activation in Newtons.

The viscoelastic parameters (KSE, KPE, B) of all muscles in the limb are determined by fitting simulated joint motion to experimental hanging leg data. Collaborating with partners at Northwestern University, skin marker data has been recorded for freely hanging rat legs in which individual muscles are stimulated by electrodes. In Animatlab, I stimulate these same muscles and compare the resulting joint motion to experimental data. Through an optimization routine, I reduce the sum squared difference of the joint angle waveforms by changing the viscoelastic properties. This process is described in further detail in the supplementary material.

## Sub Aim 2.3: Calculate muscle forces necessary to recreate motion

To recreate motion, it is necessary to develop force profiles for all muscles in the hindlimb. This is accomplished through a process in which the leg is driven through a desired leg trajectory and passive torques and moment arm profiles are measured. Passive torques include the passive tension generated by muscles and the gravitational weight of the limb segments. Moment arm profiles are generated as defined in Aim 1. Additionally, it is possible to apply load torques that simulate the effects of ground reaction forces by treating the leg as a multi-segment arm with a force vector at the end effector (Murray, Li, and Sastry 1994).

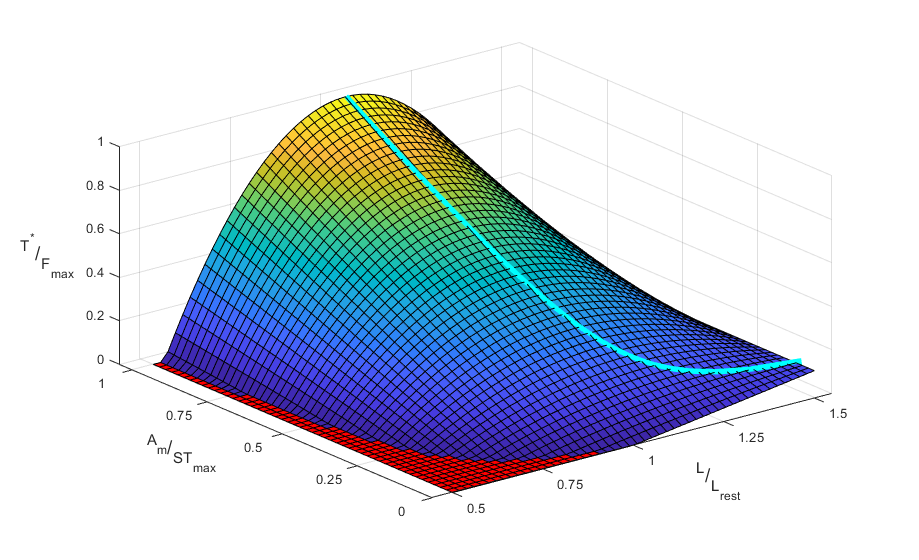
At every timestep, an optimization process is carried out such that forces counteract the passive torques, resulting in the recreated motion. Since force distribution is an infinite subspace (i.e. there are an infinite number of force combinations), different force optimization methods have been explored. Methods have been defined for minimizing total muscle force (Pedotti, Krishnan, and Stark 1978; Penrod, Davy, and Singh 1974), stress (Crowninshield and Brand 1981), activation (Kaufman et al. 1991), and fatigue (Prilutsky and Zatsiorsky 2002).

An optimization cost function was selected from Pedotti’s work, , due to its ability to create smooth tension profiles that minimized spontaneous muscle switching.

## Sub Aim 2.4: Modify the Animatlab muscle model to correct for tension deadzones

While recording tension profiles in Animatlab, it became apparent that the tension calculations contain a small error that made predicting muscle forces difficult. There are regions of length and activation in Animatlab’s default muscle tension model (Equation 1), where tension should be present but is not. This region, shown as the red surface in Figure 8, causes the tension profile to become discontinuous for valid length-activation values and misrepresents the passive response of muscle to length changes.

To determine the cause of tension deadzones, I examined the steady state muscle tension (),



**Figure 8.** A surface representing the steady state tension of a muscle as a function of its length and activation. The red surface represents a tension deadzone, an area of length and activation that is incapable of generating tension despite both values being within valid ranges. The cyan line represents the maximum steady state tension with respect to length.

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Tension deadzones are the result of allowing the passive length term, , to generate negative values when the muscle is below its resting length. This is antithetical to the concept that muscles only generate contractile tension. At moderate values near the resting length, this error does not have a large effect. However, when the muscle is significantly below the resting length, it is possible that the “negativity” of the passive tension will counteract the “positivity” of the activation.

To correct tension deadzones, I modified the tension equation in Animatlab using the software developer kit. Specifically, I changed the muscle tension in Equation to

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where denotes the ceiling function. This modification fixes the tension deadzone problem and prevents the muscle from generating negative passive tension. More detail on this correction is discussed in a 2020 Living Machines publication.

### Publications

1. Young, F., Hunt, A., Chiel, H., & Quinn, R. Using Animatlab for Neuromechanical Analysis: Linear Hill Parameter Calculation. Living Machines 2020, (n.p.)

## Sub Aim 2.5 Manuscript Proposal: Exploring the effects of viscoelastic properties on swing phase control in animals of different scales

Anecdotal observations from Dr. Boris Prilutsky indicate that at the end of swing phase in the rat, the vastus muscles (knee extensors) exhibit a burst of activity that is not seen in cats. Low level activation bursting in the rat seems to be present in the vastus lateralis in some work (Thota et al. 2005; Aoi et al. 2013) and is absent in cat EMGs (Prilutsky et al. 2015; Markin et al. 2012). This indicates that, perhaps, a rat nervous system must compensate for a lack of limb inertia by stimulating specific muscles. A possible broader implication for this observation is that the scale of an animal causes its nervous system to approach the same task in different ways to account for its body composition.

Swing phase of gait is a relatively simple limb task that has been shown to elicit different neural activation responses depending on the scale of an animal (Hooper et al. 2009; Hooper 2012; von Twickel et al. 2019). This makes it a useful activity for analyzing the impact that scaling properties have on nervous system demands. By analyzing the force demands from swing phase at different scales, we can make inferences into how the nervous system must behave in order to accommodate the proper motion. **The goal of this paper is to demonstrate that force profiles are predictably different during swing phase for animals of different scales**.

Based I hypothesize that a rat-sized model will show that propulsive muscles must be active for a relatively long duration of swing in order to pull the leg forward. In a cat-sized model, I would expect to see less propulsive muscle activity during swing phase compared to the rat. In a horse-sized model, I would expect to see braking forces during the latter part of swing in order to slow the limb down. This work would clearly demonstrate that the nervous systems of animals at different scales change their activity in a predictable manner in order to accommodate scale-dependent limb properties.

# Aim 3 – Investigate neural control strategies for task-specific hindlimb motion.

The output motion of a limb is a combination of neural control, muscular properties, and environmental state (Nishikawa et al. 2007). What kind of perturbations could a rat leg resist mechanically and what kind do they need control for? **The goal of this aim is to examine how the viscoelastic properties of a rat hindlimb are specifically suited to reject perturbations at the size and speed that rats experience while walking.** I hypothesize that the baseline viscoelastic properties of the hindlimb are specifically suited to reduce the need for neural control by minimizing the effect of these perturbations.

Perturbation response is well studied as a method for understanding how environmental effects can be accommodated by using local reflex pathways (Torres-Oviedo, Macpherson, and Ting 2006). I expect that by changing the baseline viscoelastic makeup of the hindlimb, that it will cause the limb to experience long term effects from perturbations through the limb’s inability to return to steady state (dynamic or static). For example, reducing the damping in hindlimb muscles may cause the limb to reject fast perturbations but not change the response to the size of the perturbation itself.

The use of the many-muscled model allows for high parametric fidelity in which viscoelastic parameters can be changed for individual muscle or for muscle groups. It would be possible to determine which areas of the hindlimb are primarily responsible for specific perturbation responses and to simulate the limb response if group parameters are changed or removed altogether.

## Sub Aim 3.1: Develop muscle activation profiles for arbitrary limb actions.

With the ability to calculate forces for motion, it is possible to develop a process for calculating neural activation profiles to determine what kind of input the muscle motoneurons may be receiving. To do this, we use the tension and length profiles throughout the driven motion to calculate muscle activation. It is assumed that activation profiles from this process reflect the central nervous system commands which direct motion.

## Sub Aim 3.2: Develop a Matlab toolbox for generating large-scale synthetic nervous systems

As we begin stimulating muscles through motoneurons in Animatlab’s neural design simulator, it is helpful to develop tools that can rapidly modify large groups of neurons. A Matlab toolbox, called Canvas, has been created and includes a library of Animatlab objects and their associated parameters. Object-oriented programming allows users to add and connect neurons, create new synapse types, and generate charts to plot simulation results all within Matlab. Users are then able to generate either an Animatlab project (contains the interactive user interface) or a simulation file (for direct simulation results without visualizing the physics simulation).

Large networks, such as the multi-layer CPG networks for controlling limb locomotion, can include hundreds of Animatlab objects and thousands of individual connections. Canvas reduces the time required to hand-connect networks by allowing the user to implement these systems through routines as simple as a for-loop. The modular nature of Canvas also allows users to build their own pre-fabricated networks, allowing for rapid-deployment of complex subnetworks.

## Sub Aim 3.3: Manuscript Proposal: Study perturbation response in the hindlimb with neural control included

I want to test how a leg resists without control. I define 'resisting without control' as the leg's natural response to an impulse and is characterized by the inertial/VE composition of the limb.

This knowledge would be important in control because VE parameters might be sensitive to a specific type of perturbation response. An analogous experimental preparation would be a decerebate animal such that there are no descending commands regulating limb response. VE parameters might be sensitive to perturbation magnitude, meaning that the nervous system must become active in order to compensate for only a certain size of perturbation. If this is the case, it may highlight compensatory mechanisms in the nervous system that are necessary to resume normal motion. VE parameters might be sensitive to perturbation speed, meaning that the nervous system must become active in order to compensate for only a certain speed of perturbation. If this is the case, it may indicate whether perturbation response comes from higher or lower level control systems (lower level control systems being faster to respond than higher level).

I would characterize the perturbations in the following way. One way is to consider external vs internal perturbations. Internal perturbations would require the leg to be moving in a neuron-controlled setup and then injecting a pulse into specific motoneurons. External perturbations would require the leg to be stepping or being moved externally (force plate at foot) and then injecting a mechanical pulse into the leg. If external perturbations are to be considered, then we must judge the difference between impact vs uneven ground. Considerations of uneven ground would require either that the model is stepping over uneven terrain or through simulating ground responses for even/uneven ground with a stationary leg.

Supplementary Material

## VE Parameter Optimization

To develop baseline VE parameters for the hindlimb muscles, we match experimental joint motion with simulated joint motion. This is accomplished by optimizing the parameters Kse, Kpe, and B for thirty-eight muscles to reduce the sum-squared difference between the simulated and experimental joint motion profiles.

In addition to matching experimental results, it is important that the VE parameters are selected such that they maintain the functional goals for muscles in Animatlab. For a maximal (20 nA) stimulus, we want the muscle to be capable of generating its maximum tension (Fmax) while at steady state. When not stimulated (0 nA), the muscle tension should be purely passive (Am = 0).

The optimizer for this process is the patternsearch function in Matlab. This process perturbs input values in a “mesh” pattern in order to find parameter combinations that reduce a cost function. Patternsearch is useful for problems that do not have a defined gradient, such as a simulation with discrete outputs. In addition to using the mesh polling method, a mesh adaptive direct search is included to increase effectiveness by performing an additional search step before polling for new values.

Linear constraints are applied to the optimizer to ensure that the tension profiles in Animatlab do not become asymptotically unstable. The discrete representation of the muscle tension is

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At each timestep, the previous tension value, , is multiplied by a constant. To prevent asymptotic instability (i.e. oscillations that cause the tension to increase boundlessly), this constant must be bounded. These linear constraints ensure that the physics timestep constraint,

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is true for all muscles. This limitation is described in more detail in a 2020 Living Machines paper.

## ST Parameter Derivation

The activation parameter, Am, represents a sigmoidal relationship between stimulus and tension which is important for controlling muscles by applying voltage to the motoneuron. Specifically, the maximum value of Am (STmax) and the steepness of the ST slope have the largest impact on the relationship between stimulus and tension. The stimulus-tension equation takes the form

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where S is steepness, xoff is the voltage offset (set to -50mV for all muscles), V is the motoneuron voltage, and yoff is the output offset. The range for the ST-curve is defined as [-60, 40] mV in order to interface with functional subnetwork neurons defined from prior work (Szczecinski, Hunt, and Quinn 2017).

Originally, I set the ST output range to [0, 1.05Fmax] and then determined the necessary stiffness for each muscle. The motivation for this method was to establish a range in which STmax was slightly larger than Fmax with the belief that the Am parameter would then be able to generate all values up to the maximum tension. However, these values required a curve steepness that was quite large (~1200), resulting in a steep curve with a form similar to that in Figure 10.



**Figure 10** A steeper ST-curve causes the muscle to behave like a switch.

The issues with a steep ST-curve using the output values as defined above are twofold. First, the tension generating capabilities of motoneuron stimulation are inhibited by a term in the tension equation which reduces the output range of the ST-curve. Second, the steeper the ST-curve is, the more it behaves like a switch.

When running experiments where the hindlimb is actuated by muscle stimulation, I noticed that the maximum tension for any muscle was much smaller than Fmax. This limited the tension output and made the leg weaker than it could be. The reduced output is related to the term  in the tension equation. Essentially, this term inhibits tension generation, while Am is trying to increase it. To address this issue, the value of STmax is dynamically set based on the viscoelastic parameters of the muscle in order to balance the inhibitory tension term with the activation term.

Steady state muscle tension is a function of length and activation,

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At resting length, the steady state tension becomes

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To generate maximal tension through motoneuron activation, the STmax is set such that

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This assumes that at steady-state resting position, the muscle can generate Fmax by stimulating the motoneuron. This approach can create values of STmax that are dramatically larger than Fmax, exacerbating the switch-like behavior related to curve steepness.

It is difficult to create smooth motoneuron-driven motion with a steep curve because muscle tension tends to switch on and off rather than gradually shift values during stride. To address this issue, I decided to set the curve steepness to a specific value for all muscles such that the switch-like behavior is reduced. To accomplish this, I reduced the ST-curve output range slightly to [0, .98STmax]. To find the necessary steepness for this range, we solve equations at the end values.



which results in values of  and . Now, when I set Kse, Kpe, and B for each muscle, I also set ,, and S = 459.5.

## References

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