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Exploring the high-dimensional structure of muscle redundancy via subject-specific and generic musculoskeletal models

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ABSTRACT

Subject-specific and generic musculoskeletal models are the computational instantiation of hypotheses, and stochastic techniques help explore their validity. We present two such examples to explore the hypothesis of muscle redundancy. The first addresses the effect of anatomical variability on static force capabilities for three individual cat hindlimbs, each with seven kinematic degrees of freedom (DoFs) and 31 muscles. We present novel methods to characterize the structure of the 31-dimensional set of feasible muscle activations for static force production in every 3-D direction. We find that task requirements strongly define the set of feasible muscle activations and limb forces, with few differences comparing individual vs. species-average results. Moreover, muscle activity is not smoothly distributed across 3-D directions. The second example explores parameter uncertainty during a flying disc throwing motion by using a generic human arm with five DoFs and 17 muscles to predict muscle fiber velocities. We show that the measured joint kinematics fully constrain the eccentric and concentric fiber velocities of all muscles via their moment arms. Thus muscle activation for limb movements is likely not redundant: there is little, if any, latitude in synchronizing alpha–gamma motoneuron excitation–inhibition for muscles to adhere to the time-critical fiber velocities dictated by joint kinematics. Importantly, several muscles inevitably exhibit fiber velocities higher than thought tenable, even for conservative throwing speeds. These techniques and results, respectively, enable and compel us to continue to revise the classical notion of muscle redundancy for increasingly more realistic models and tasks.

1. Introduction

This invited paper has the dual purpose of being didactic about computational methods to test neuromechanical hypotheses in the context of high-dimensional subject-specific and generic models, and applying these methods to explore the classical notion of muscle redundancy, a central tenet in our field. This is made possible by computational geometry and stochastic techniques we have been developing to understand the interactions among (i) model topology (the number and type of connectivity among the elements of the model); (ii) parameters values (the individual and specific numerical values assigned to each model parameter); and (iii) the requirements of real-world tasks for tendon-driven biomechanical systems with numerous kinematic degrees of freedom and muscles.

The notion of computational models as instantiations of specific hypotheses, the stochastic exploration of model capabilities to test these hypotheses, and the relationship between generic vs. subject-specific models have been addressed elsewhere (Keenan and Valero-Cuevas, 2007; Rieffel et al., 2010; Valero-Cuevas et al., 2007a, 2009a, 2007b). However, increasing the physiological realism and utility of these techniques requires extending them to ever higher dimensions (i.e., larger numbers of muscles and kinematic degrees-of-freedom, DoFs), and to real-world tasks involving the production of static forces and fast motions—while limiting computational cost. But working with ever-greater numbers of muscles and DoFs inevitably challenges our ability to visualize the complex and high-dimensional structure of the set of feasible muscle activation patterns. It also significantly challenges our ability to find unique solutions (if they even exist) to these computational problems, or defend their optimality/uniqueness.

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We have found these stochastic modeling techniques particularly useful to test the classical notion of muscle redundancy, which has often been called the central problem of motor control (Bernstein, 1967). The classical notion of muscle redundancy is thought to arise by virtue of having (many) more muscles than DoFs. With many muscles acting upon the same number or fewer joints, some argue that the central nervous system (CNS) must solve an optimization problem to select and implement specific muscle activation patterns from a theoretically infinite set of possibilities (Prilutsky, 2000; Scott, 2004), while others argue that near- or sub-optimal solutions are good enough (Loeb, 2012; Valero-Cuevas et al., 2009b). If fewer muscles actuated a limb, the arguments go, feasible forces and motions could still be produced without significant need for such optimizations.

Many of us have argued that this classical interpretation of the number of muscles in vertebrate limbs is paradoxical with respect to evolutionary biology and the clinical reality of motor dysfunction: extant vertebrates tend to have many more muscles than DoFs, even though it is energetically expensive to develop and maintain muscle mass—and injury to even a few muscles can cause dysfunction. Using the same argument of energetic efficiency invoked for optimization in motor control—but at the scale of evolutionary time—we, and others, have argued that we likely have barely enough muscles for versatile real-world behavior (Keenan et al., 2009; Kutch and Valero-Cuevas, 2011, 2012; Loeb, 2000; Talati et al., 2005). This view is closely aligned with the computational neuroethology approach (Arbib, 1987; Beer, 1990; Cliff, 1990) that argues that perhaps we need all our muscles because of the sheer variety of tasks—each distinguished by the type and number of constraints they must meet—over the course of a day/week/lifespan. Put differently, if we have too many muscles in our limbs, which ones would you like to donate or paralyze? Therefore, it is important that our research into muscle redundancy work toward reconciling these different views.

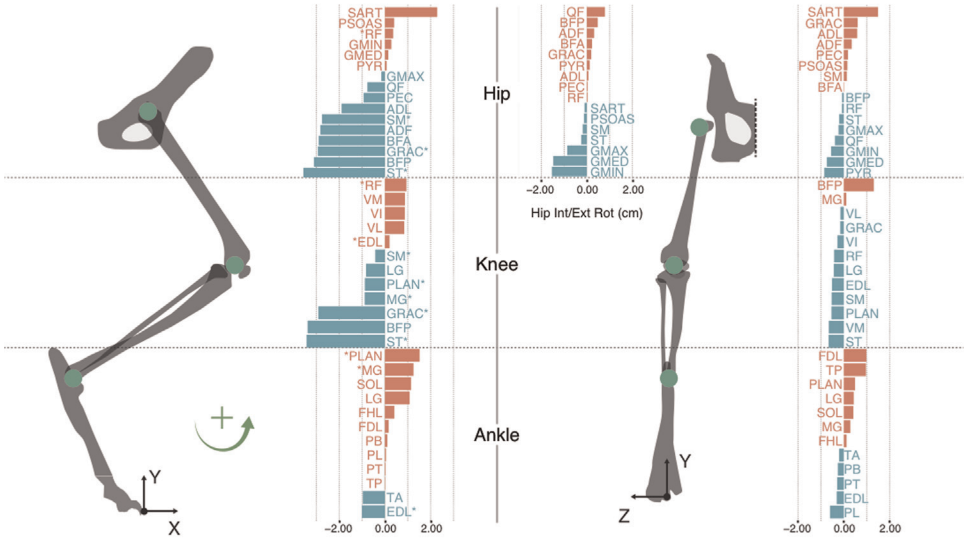
Still, for most tasks in healthy individuals, some redundancy is bound to remain; regions of feasible activation solutions that are not a single point will consist of a neighborhood or subspace that naturally contains an infinite number of solutions (i.e., points). The nervous system is still confronted with the need to choose a specific solution to implement at any point in time; however, that collection of feasible solutions remains highly structured due to both the mechanics of the limb and the constraints of the task (Bizzi and Cheung, 2013; Kutch and Valero-Cuevas, 2011, 2012; Sohn et al., 2013; Tresch and Jarc, 2009; Valero-Cuevas et al., 1998). The purpose of this work, therefore, is to begin to address the need posed by us (Kutch and Valero-Cuevas, 2011, 2012; Valero-Cuevas et al., 1998), and others (Loeb, 2000; Sohn et al., 2013; Tresch and Jarc, 2009), to improve computational methods for understanding and visualizing the dimensionality and structure of feasible solutions sets for limbs with large numbers of muscles performing tasks with realistic constraints. Here we do so for 3-D musculoskeletal models of a cat hindlimb and a human arm with 31 and 17 muscles, respectively, using MATLAB (v2013b, The Mathworks, Natick MA).

2. Cat hindlimb model: methods

The purpose of this cat hindlimb model is to present a novel way to visualize the structure of the set of all feasible muscle activations to produce maximal and submaximal static paw forces in every 3-D direction. In addition, we compare solutions among three subject-specific models to explore the effect of between-subject anatomical variability on muscle activation. The models consist of three feline (*Felis catus*) hindlimbs, each with 31 muscles actuating 7 kinematic DoFs from the hip to the ankle. We used the bone lengths and moment arms for the cat hindlimbs originally presented by McKay and Ting. (2008), and modified by Sohn et al. (2013), that were graciously shared with us by the authors. The species average model for the cat hindlimb is shown in Fig. 1.

2.1. Feasible force and feasible activation sets for cat hindlimb model

As described in detail elsewhere (e.g., McKay et al., 2007; Valero-Cuevas, 2009; Valero-Cuevas et al., 1998), a feasible force set (FFS) describes the set of all static forces that can be produced at the endpoint of a limb. Briefly, the feasible mechanical output of the endpoint of a limb is 6-dimensional: 3 forces (the FFS) and 3 torques (the feasible output torque set)—which arises from the fact that a rigid body (i.e., the endpoint of a limb) has six DoFs, three displacements, and three rotations. Together they form the 6-dimensional feasible output wrench (Murray et al., 1994). In the robotics literature (Miller et al., 2005), feasible force and torque outputs are plotted separately as they have different units. Thus



a. Sagittal view of right hind limb b. Frontal view of right hind limb

Fig. 1. Bone lengths, joint axes of rotation, and moment arm matrix for the species average cat hindlimb model, in cm. Positive values are shown in red and negative values in blue, as per the right-hand-rule. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)