

BIOMECHANICS TO BRAIN: UNRAVELING THE COMPLEX NEURAL CONNECTIVITY OF MULTI-MUSCLE CONTROL

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INTRODUCTION

Understanding how the CNS orchestrates the activity in hundreds of muscles to successfully control the human body is a long-standing problem that has generated both scientific and clinical interest [1-3]. The issue is how the CNS selects a muscle coordination pattern from an infinite set of options [4], and how it plausibly implements this pattern in neural connectivity.

Research on this problem has been dominated by the idea that the CNS can not activate a large number of muscles to perform functional tasks before it combines the muscles into a small number of groups, referred to as muscle synergies [5-7]. However, my research has shown that index finger muscles are not controlled using synergies [8], that certain synergies are biomechanically mandated rather than neurally-chosen [9], and that experimentally-observed muscle synergies during movement and force production may reflect a mixture of biomechanical and neural constraints [10].

Here, I propose that complexity in neural structures for multi-muscle control, including the genesis of muscle synergies, results not from a principle of reducing the number of degrees-of-freedom to be controlled, but from the biomechanical need to represent posture-dependent changes in muscle action across multiple joints. I prove this by showing that simple neural connectivity schemes without muscle synergies can readily learn to control large numbers of muscles, but that the resulting networks are not effective at controlling the limb if the posture changes.

METHODS

Our biomechanical analysis of neural connectivity relies on understanding the transformation of muscle force to endpoint force, and how this transformation changes with posture. We used cadaveric hands to directly measure the transformation from muscle force to index fingertip force (the *action matrix*), as

in prior work [11], for all 7 tendons controlling the index finger (FDS, FDP, EI, EDC, FDI, FPI, LUM) (Figure 1A). We measured the action matrix for a variety of index finger postures in two specimens.

To ensure our results generalized to systems with many more muscles, we assembled a sagittal plane model of the human leg using anthropometric measures [12] and moment arms for 44 muscles [13] (Figure 1B). A posture-dependent action matrix was calculated using standard techniques [14].

We inferred the most basic network necessary to transform neural representations of desired endpoint force into the muscle forces necessary to achieve the desired endpoint forces. This network contains weighted connections between the components of the desired endpoint force and the motor pool of each muscle controlling the limb. The appropriate weights were learned using a simple gradient descent algorithm attempting to minimize the combined cost of making errors in endpoint forces and using too much energy, defined to be the sum of squared muscle forces. We evaluated how well a network generalized by learning the connection strengths at one posture, and attempting to have the network generate the correct endpoint forces at a different posture. This analysis was performed for both the cadaveric measurements and the leg model.

RESULTS AND DISCUSSION

We found that, not unexpectedly, networks with random (naive) connections generated large errors between the desired and actual endpoint force (Figure 1C). However, we found, surprisingly, that a simple learning algorithm could mature the connection strengths in this network to correctly activate the muscles to produce the desired endpoint forces with minimum muscle effort (Figure 1D). Unfortunately, the mature network for one posture could not produce the desired endpoint forces in a different posture (Figure 1E). We observed this lack of generalization across posture for both the leg model, and the

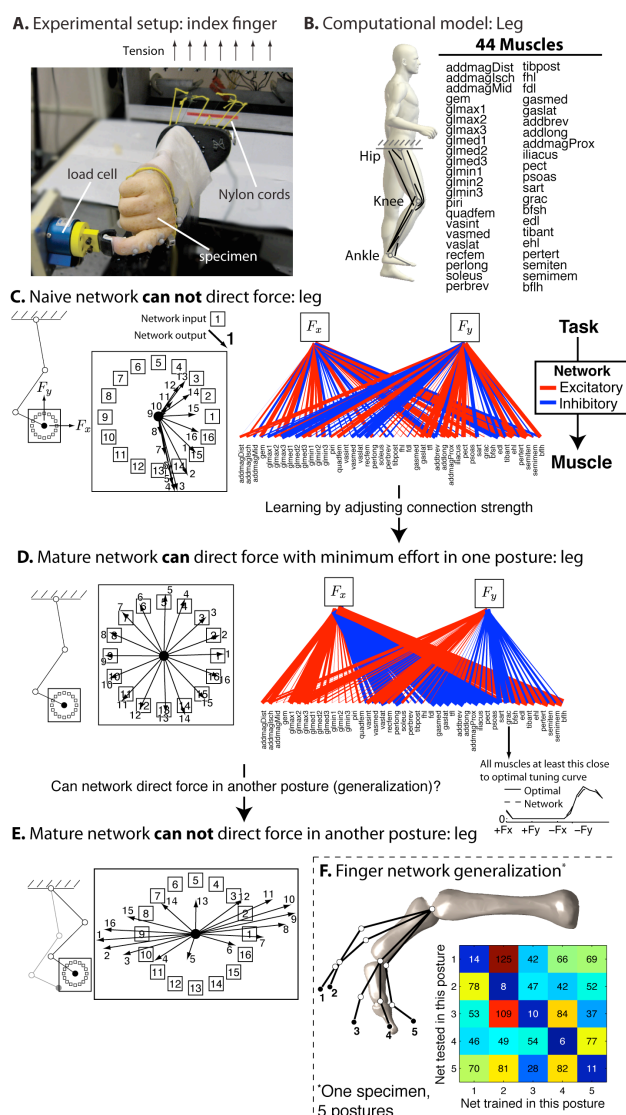


Figure 1. Muscles can be activated by simple networks, but these networks do not generalize across posture. Please see text.

cadaveric measurements, where errors in output force could be 125% or more in both specimens (Figure 1F).

Our current understanding of the neural connectivity that drives multi-muscle control is dominated by the notion that the brain must simplify the highly-redundant musculature into task-relevant groups [7]. This is believed to be accomplished by functional units called muscle synergies, perhaps encoded in the spinal cord [15], that act as an intermediary between task goals and muscle activations. Here we have shown that the intermediary of muscle synergies is not necessary from the standpoint of simplification - desired endpoint forces can be mapped directly to the force required in each of a large number

of muscles, and the appropriate connection strengths in this mapping can be learned with simple rules.

These results open a new direction in multi-muscle control research, because muscle synergies, as intermediaries between task-level and muscle-level commands, could be re-interpreted as the necessary elements to perform posture-dependent switching. The results of this study can be used to formulate new hypotheses about the nature of multi-muscle control networks, motivated by an understanding what neural structures are biomechanically mandated.

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