Muscle redundancy does not imply robustness to muscle dysfunction

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ABSTRACT

It is well-known that muscle redundancy grants the CNS numerous options to perform a task. Does muscle redundancy, however, allow sufficient robustness to compensate for loss or dysfunction of even a single muscle? Are all muscles equally redundant? We combined experimental and computational approaches to establish the limits of motor robustness for static force production. In computer-controlled cadaveric index fingers, we find that only a small subset ($< 5\%$) of feasible forces is robust to loss of any one muscle. Importantly, the loss of certain muscles compromises force production significantly more than others. Further computational modeling of a multi-joint, multi-muscle leg demonstrates that this severe lack of robustness generalizes to whole limbs. These results provide a biomechanical basis to begin to explain why redundant motor systems can be vulnerable to even mild neuromuscular pathology.

1. Introduction

Muscle redundancy – having more muscles than mechanical degrees-of-freedom (DOFs) – has long been a central problem in biomechanics and neural control. At issue is how the central nervous system (CNS) selects muscle coordination patterns from a theoretically infinite set of possibilities (Bernstein, 1967). Little attention, however, has been given to the related critical clinical question of whether muscle redundancy grants the body robustness to dysfunction of even one muscle. Thus advancing motor systems research requires that we clarify the relationship between muscle redundancy and robustness to muscle dysfunction.

While muscle redundancy theoretically affords muscles infinitely many activation levels for a given sub-maximal task, the range of these valid activation levels has critical implications to robustness. For example, if muscle A can produce any force within a 10 N range for a particular task (i.e., an infinite number of possible activation levels), the implications to robustness are critically different if this range is 0–10 N or 5–15 N. If the former case, muscle A is redundant because the CNS can find valid coordination patterns even if it is lost (activation=0). However, in the latter case, muscle A is necessary, because the CNS cannot adapt to its loss: there are no valid coordination patterns if muscle A is sufficiently weakened or lost. Here we present

computational geometry methods that identify muscles that are necessary for specific tasks. By studying both human fingers and legs, we find that tendon-driven biomechanical systems exhibit surprisingly little robustness to dysfunction of even one muscle, and show how these computational methods open up numerous novel research avenues in biomechanics and neural control.

2. Methods

We studied the necessity of muscles by analyzing the static transmission from muscle force to endpoint output. For the human index finger, we measured that transmission experimentally by applying known tensions to its seven tendons in cadaveric hand specimens while recording the resulting fingertip forces. For the human leg, we used published data to construct a biomechanical model of the hip, knee, and ankle in the sagittal plane to predict the force vector produced at the foot by maximal activation of each muscle. In each case, we derived an action matrix **A** that maps a vector $\vec{a}$ describing the activation in each muscle to the force output of the limb (Murray et al., 1994; Valero-Cuevas, 2005b). Such a linear transformation has been found to be valid for a fixed posture of a finger (Valero-Cuevas et al., 2000, 1998) and leg (Kuo and Zajac, 1993).

2.1. Action matrix for human index finger

We resected four fresh frozen cadaver arms at the mid-forearm level and dissected them to reveal the proximal end of the insertion tendons of all seven muscles controlling the index finger as in our prior work (Valero-Cuevas et al., 2000): flexor digitorum profundus (FDP), flexor digitorum superficialis (FDS), extensor indicis (EI), extensor digitorum communis (EDC), first lumbrical (LUM), first dorsal interosseous (FDI), and first palmar interosseous (FPI). We fixed the specimen rigidly to a tabletop using an external fixator (Agee-WristJack, Hand Biomechanics Lab, Inc., Sacramento, CA), and we tied and glued the proximal tendons to nylon cords attached to rotational motors. Motors were controlled using a real-time controller and custom-written software. Load cells measured the

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