BIOMECHANICAL AND EXPERIMENTAL CONFOUNDS TO THE DETECTION OF NEURALLY-GENERATED MUSCLE SYNERGIES

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INTRODUCTION

A hypothesis that has received considerable attention is that the CNS activates muscles in patterns (synergies) so as to reduce the number of control degrees-of-freedom (DOF). Such covariation has been detected as a reduction in the dimensionality of muscle activations in a number of experimental paradigms, including cat postural control [1], human postural control [2], human arm control [3]. While such dimensionality reduction in muscle activations is commonly observed, there exist counterexamples [4, 5], and the non-neural sources that could contribute to such covariation (e.g., plant biomechanics, task constraints, and the choice of motor outputs selected by the experimenter) have received little rigorous study. Here we set out to establish the extent to which non-neural sources enforce muscle synergies.

More specifically, several studies have attempted to control for these confounds by requiring the production of circular or spherical (i.e., omnidirectional) force output (e.g. [3, 6]). Unfortunately, a rigorous computational geometric analysis proves that, for many realistic distributions of muscle mechanical action across multiple joints, omnidirectional force tasks are an insufficient test of neural synergies. This is because omnidirectional outputs unavoidably constrain muscle activity patterns to a low-dimensional subspace, even in the absence of any neural constraints.

METHODS

We analyzed the transformation from tendon tension to endpoint force of the human index finger measured in cadaveric specimens. In this experimental paradigm [7, 8], we rigidly attach the fingertip to a 6 degree-of-freedom load cell and apply known tensions to each of the 7 tendons of the index finger (FDS, FDP, EI, EDC, FDI, FPI, LUM). We apply every one of the 128 possible combinations of 10 and 1 N tension across tendons in random order. We linearly regress the resulting endpoint forces against the tendon tensions to determine the 3×7 *action matrix* for the finger, whose *i*th column is the 3-dimensional endpoint force resulting from applying 1 N to the *i*th tendon.

Applying established methods in computational geometry [9, 10] to the action matrix, we compute the set of all muscle activation patterns that can feasibly produce endpoint forces on a circle in the plane of finger flexion-extension. We then calculate the dimensionality of these muscle activations using principal components analysis (PCA).

RESULTS AND DISCUSSION

The action vectors for all 7 muscles were distributed over endpoint force space so as to enable the production of force in any direction (Figure 1A). For a set of forces spanning all directions in the plane of finger flexion-extension (Figure 1B), we computed the dimensionality of the set of muscle activations that could have feasibly generated these forces (Figure 1C). We found that the requirements of this task and the distribution of the action vectors suffice to constrain the feasible muscle activations to a low dimensional subspace of the 7-dimensional muscle activation space. Three principal components explain > 80% of the muscle activation space variance (Figure 1C).

These results challenge the tendency in sensorimotor neuroscience to attribute low-dimensionality in muscle activation to neural

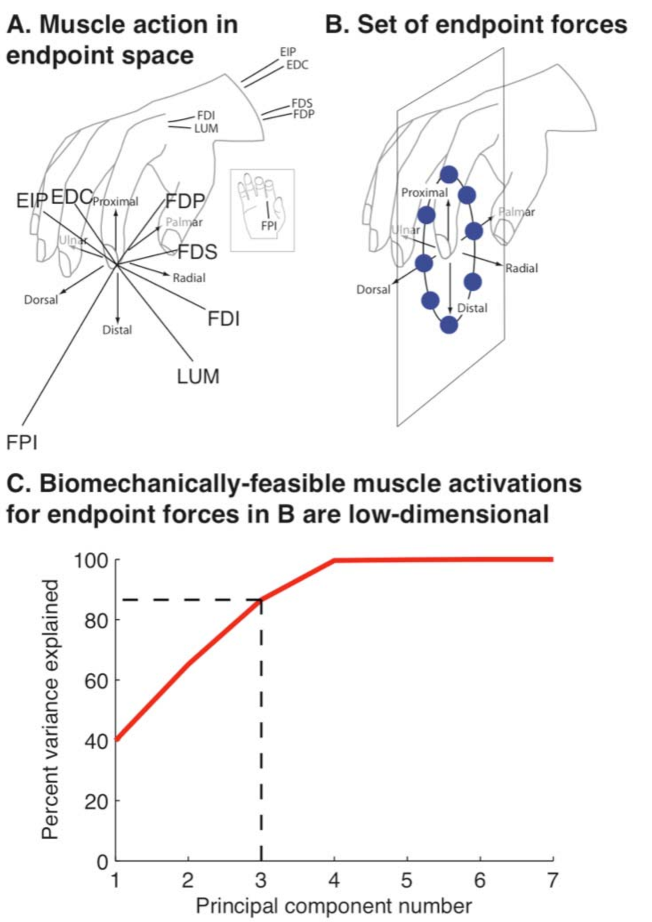

Figure 1: A. Action vectors for all muscles. B. Target endpoint forces. C. Dimensionality of feasible activation set.

constraints. Experiments that exhaustively explore omnidirectional force production in a circle (or sphere, Figure 1B) *do not* necessarily remove non-neural confounds.

The non-neural confounds described in this study show the need to look beyond structure in average muscle activations. Recent studies have suggested that natural variability produced by humans during motor tasks may be rich in information about neurally-generated muscle synergies [4, 5, 11].

These results compel us to develop novel experimental approaches that can conclusively establish the neural contributions to muscle synergies. Dimensionality reduction of neural origin can only be advocated after removing non-neural confounds [12]. Given that generating sufficiently many force outputs is likely to be experimentally prohibitive, leveraging experimental data with computational models can help establish the amount of dimensionality reduction attributable to the neural controller.

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