Spike recordings from the primary motor cortex correlate more strongly with individual muscles or original joint angles than with muscle synergies or joint angle PCs

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Introduction

High-dimensional muscular or kinematic spaces can be reduced mathematically to low-dimensional synergies which capture most of the original variance. Such synergies can reduce the computational burden of controlling neuro-prosthetic devices. The extent to which such synergies are used in natural neural control, and if so, which parts of the central nervous system generates synergies, remains uncertain.

We tested the hypothesis that muscle synergies or kinematic synergies are represented in primary motor cortex (M1) neurons. Spatial (time-invariant) muscle synergies, spatiotemporal (time-varying) muscle synergies, and joint angle principal components were extracted from recordings during a reach-to-grasp task. We compared the correlation between synergies and spike activity with the correlation between individual muscles or joint angles and spike activity.

Methods

Experimental Setup

Three rhesus monkeys (*Macaca mulatta*, L, X, and Y) were trained to perform a reach-to-grasp task. Subjects were cued to reach to one of four objects: mallet, pull handle, push button, or sphere. These objects were located in one of eight radial locations. The behavioral task was controlled by custom software written in TEMPO (Reflective Computing, Olympia, WA).

Chronic, intramuscular bipolar electrodes were implanted in right forearm muscles (L: 14 muscles; X: 15 muscles; Y: 12 muscles) to record electromyographic (EMG) activity. Twenty-two angles of joints in the arm and hand motion as 22 joint angles were derived from 36 optical markers tracked with a motion capture system (Vicon Motion Systems, Oxford, UK). Each monkey was implanted with floating microelectrode arrays (FMAs; MicroProbes, Gaithersburg, MD) in M1. Each FMA consisted of 16 parylene-C insulated platinum/iridium recording electrodes of various lengths between 1 and 9 mm.

Neurophysiological signals were digitized and hardware filtered using a Plexon data acquisition system (Plexon, Dallas, TX). Offline analyses were performed in MATLAB (MathWorks, Natick, MA). All data were downsampled to 100 Hz, aligned on the onset of movement, and restricted to a fixed window of -0.15 to 0.45 s.

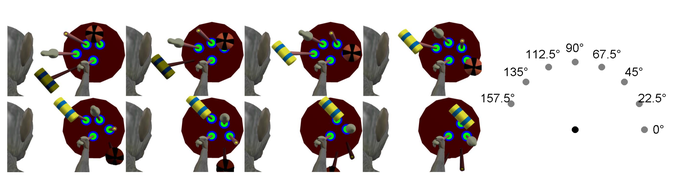


Figure 1. Reach-to-grasp task. To position the objects at different locations, the apparatus was rotated among eight zones during each session. The eight possible locations for a given object spanned 157.5°. Objects not positioned at one of these locations with the apparatus in a given zone (darkened in the figure) were not included in the task due to mechanical or visual restrictions. (Illustration created with MSMS software courtesy of R. Davoodi and G. Loeb)

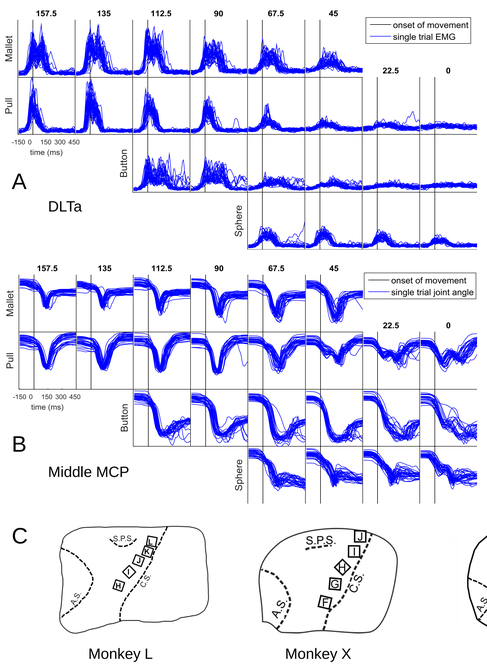


Figure 2. The reach-to-grasp task required a wide range of variety in EMG and kinematic activity. A) EMG activity (anterior deltoid), and B) Joint position (middle MCP flexion/extension) of all trials from a single recording session as a function of time. C) Simultaneously with EMG and hand motion recordings, single-unit or multiunit spikes were recorded from FMAs implanted in the primary motor cortex of each monkey.

Results

Principal component analysis (PCA) of joint angle kinematics

We extracted kinematic PCs from 22 joint angles. Six PCs accounted for ≥ 90% of the variance in joint angles. We used a comparable number of muscle synergies to explain 85% of the variance in EMG during the spatial muscle synergy analysis.

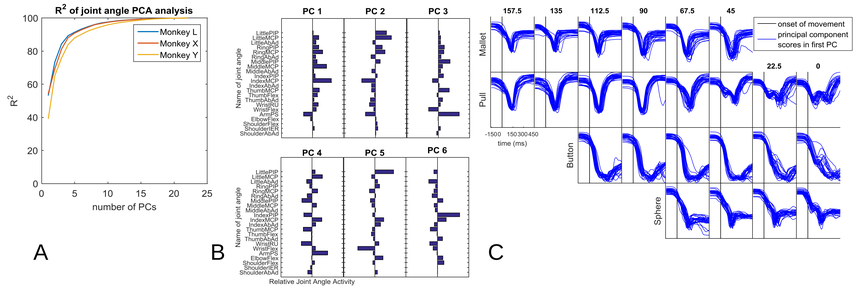
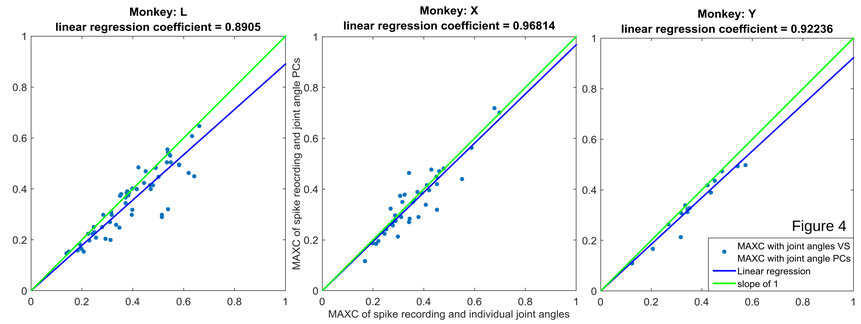


Figure 3. A) Cumulative variance explained (R^2) by joint angle principal components. Six PCs explained 90% of variance in the original joint angle activity for each animal. B) The components of the first 6 PCs from monkey L. C) PC1 activation in different location/object combinations.

If synergies are represented preferentially in the primary motor cortex (M1), we hypothesize that the activity of M1 neurons should correlate more strongly with synergies than with the original joint angles or the muscles from which the synergies were extracted.

For each single-unit or multiunit spike recording, we cross-correlated firing rate with i) each of the 22 original joint angles, ii) each of the first 6 PCs, over leads and lags of ± 400 ms. We then compared the maximal absolute value of the cross-correlation (MAXC) achieved with any original joint angle to the MAXC achieved with any joint angle PC.

Across the population of significantly correlated spike recordings from each monkey, MAXCs with individual joint angles were greater than MAXCs with kinematic PCs (Wilcoxon signed rank tests with H_0: $MAXC_{\text{joint angle}} \leq MAXC_{\text{PC}}$, and H_1: $MAXC_{\text{joint angle}} > MAXC_{\text{PC}}$, monkey L: p = 2.43e-7 , monkey X: p = 0.04 , monkey Y: p = 1.53e-4).



Using MAXCs with individual joint angles as predictors and MAXCs with kinematic synergies as responses, we performed linear regression analysis on significantly correlated units of each animal. The linear regression coefficients were less than 1 in all three animals (Figure 4), indicating that the MAXCs with individual joint angles are greater than the MAXCs with kinematic PCs. These results fail to support the notion that kinematic synergies are represented in the primary motor cortex.

Spatial (time invariant) muscle synergy

We extracted spatial (time invariant) muscle synergies from the original EMG recordings with non-negative matrix factorization:

$$Eqn.1 \qquad \mathbf{m}(t) = \sum_{i=1}^{N} c_i(t)\,\mathbf{w}_i$$

$\mathbf{m}(t)$ is the D-dimensional time function of EMG activity; $\mathbf{w}_i$, the i-th spatial synergy is a D-dimensional non-negative time invariant vector, specifying the relative activation level of muscles; and $c_i(t)$ is the time-varying activation coefficients of i-th synergy.

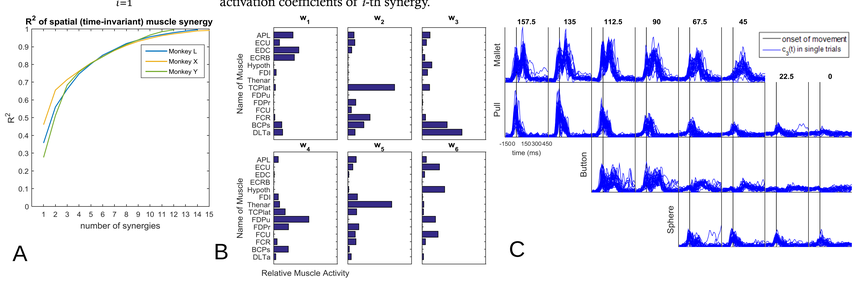
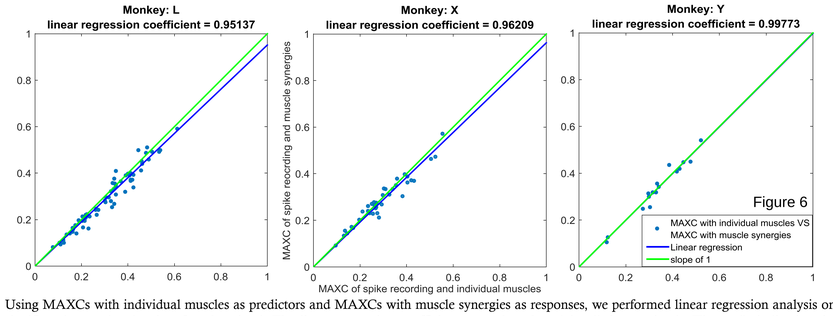


Figure 5. A) Variance explained (R^2) by spatial muscle synergy as a function of the number of synergies. Six synergies explained 85% of the variance in the original EMGs. B) six synergies from monkey L, each synergy is a muscle coactivation pattern. C) monkey L's third synergy activation coefficients $c_3(t)$ as a function of time during reach-to-grasp for each of the location/object combinations.

For each single-unit or multiunit spike recording we cross-correlated firing rate with i) each muscle's rectified EMG, and ii) each of the 6 muscle synergies. We then compared the MAXC achieved with the activity of any muscle to the MAXC achieved with any muscle synergy.

Across the population of significantly correlated spike recordings, none of three monkeys' MAXCs with muscle synergies were significantly greater than MAXCs with individual muscles (Wilcoxon signed rank tests with H_0: $MAXC_{\text{muscle}} \geq MAXC_{\text{synergy}}$, H_1: $MAXC_{\text{muscle}} < MAXC_{\text{synergy}}$, monkey L: p = 1; monkey X: p = 0.85; monkey Y: p = 0.59). In monkey L, however, MAXCs with individual muscles were significantly greater than MAXCs with muscle synergies (Wilcoxon signed rank tests with H_0: $MAXC_{\text{muscle}} \leq MAXC_{\text{synergy}}$, H_1: $MAXC_{\text{muscle}} > MAXC_{\text{synergy}}$, monkey L: p = 4.94e-7, monkey X: p = 0.16, monkey Y: p = 0.43*)*.



Using MAXCs with individual muscles as predictors and MAXCs with muscle synergies as responses, we performed linear regression analysis on significantly correlated units of each animal. The linear regression coefficients were less than 1 in all three animals (Figure 6), indicating the MAXCs with individual muscles are greater than the MAXCs with muscle synergies. These results fail to support the notion that muscle synergies are represented in the primary motor cortex.

Spatiotemporal (time-varying) muscle synergy

We extracted spatiotemporal (time-varying) muscle synergies from the original EMG recording with non-negative matrix factorization:

$$Eqn.2 \qquad \mathbf{m}(t) = \sum_{i=1}^{N} c_i\,\mathbf{w}_i(t - t_i)$$

$\mathbf{w}_i(t)$, i-th spatiotemporal synergy, is a collection of muscle activation waveforms, and c_i and t_i are the amplitude coefficient and time delay of i-th synergy.

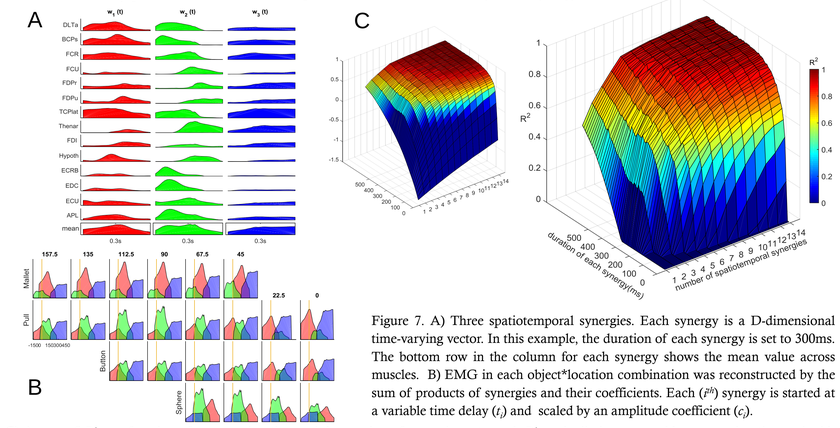


Figure 7. A) Three spatiotemporal synergies. Each synergy is a D-dimensional time-varying vector. In this example, the duration of each synergy is set to 300ms. The bottom row in the column for each synergy shows the mean value across muscles. B) EMG in each object*location combination was reconstructed by the sum of products of synergies and their coefficients. Each (i^{th}) synergy is started at a variable time delay (t_i) and scaled by an amplitude coefficient (c_i).

C) A map of R^2 as a function of synergy duration and the number of synergies extracted. R^2 gradually increases with synergy duration and with the number of synergies. Previous studies of spatiotemporal muscle synergies have selected the number of synergies based on a sharp bend in the curve of R^2 as a function of the number of synergies using a single synergy duration. In our data there is no such sharp bend appeared to indicate a specific number of synergies for any of the durations tested.

Discussion

- Our results fail to support the notion that kinematic synergies (joint angle PCs) or spatial muscle synergies are represented in the primary motor cortex.
- Examination of R^2 as a function of both the number of synergies and synergy duration revealed no specific number or duration of spatiotemporal muscle synergies in our data.
- Muscle or movement synergies may be generated from other centers of the motor system, such as the pontomedullary reticular formation and/or the spinal gray matter, while M1 neurons sculpt synergies so as to individuate movements.
- Task and/or biomechanical constraints may influence the synergies extracted by the current methods.

Acknowledgments

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