Abstract— Because of the redundancy in the musculoskeletal system, to generate a force at the hand in a given direction and with a given magnitude the central nervous system (CNS) has to select one of infinitely many possible muscle activation patterns. What strategies and constraints underlie such selection is an open and debated issue. The CNS might select muscle activations that optimize some performance criterion, such as accuracy or effort, or it might simplify the solution by constraining it to be a combination of a few muscle synergies. Flexible optimization of individual muscle recruitment or muscle synergies should give rise to distinct directional tuning of muscle activations. In this study we compared the activation of arm muscles observed during the generation of isometric force at the hand in 16 different directions with the activation predicted by flexible recruitment of individual muscles selected, for each direction, minimizing the sum of squared muscle activations and by flexible recruitment of a set of muscle synergies, by minimization of the sum of squared synergy activations. Muscle synergies were identified from the recorded muscle pattern using non-negative matrix factorization. To perform both optimizations we approximated the mapping between muscle activations and end-point force with a matrix that we estimated using multiple linear regression. We found that, in most cases, the synergistic model predicted the observed directional tuning with smaller error than the flexible model. While this result might be due to some of the assumptions and approximations used in the models, it supports the hypothesis that the CNS employs a small number of muscle synergies to simplify the control of the many degrees-of-freedom of the musculoskeletal apparatus.

I. INTRODUCTION

A long standing question in neuroscience is how the CNS coordinates the large number of degrees-of-freedom of the musculoskeletal system to achieve a variety of goals [1]. One possibility is that CNS optimizes task specific muscle activations according to some performance criterion, such as effort or accuracy, without imposing any constraint on the muscle patterns, i.e. flexibly [2-4]. Alternatively, to overcome the complexity inherent in a system with many non-linear, compliant actuators acting on multiple skeletal segments, the CNS might reduce the number of degrees-of-freedom it has to control directly by using a small number of muscle synergies, coordinated recruitment of groups of muscles with specific activation balances or profiles [5-9]. Flexible combination of these synergies would generate muscle activations that are adequate, yet not necessarily optimal, for a variety of goals.

Whether muscle synergies are a simplifying control strategy, actually employed by the CNS, or they only represent a parsimonious description of the regularities in the motor output, generated by a non-synergistic controller and due to specific task constraints, is an open and debated issue [3, 10-13]. Evidence for muscle synergies as neural control strategies comes from the observation of low-dimensionality in the muscle patterns—in many species and behaviors the muscle patterns recorded in a variety of conditions can be reconstructed by a combination of a small number of muscle synergies [6, 9, 14-20] and from neural recordings and stimulation [7, 21-24]. A recent study has argued against muscle synergies in the generation of planar isometric forces [3]. It compared the directional dependence of the covariance of the force fluctuations observed experimentally with the directional dependence predicted by either a synergistic model of muscle activation or a model assuming flexible activation of individual muscles. Indeed, it is possible to predict the muscle pattern generating a specific force according to the two models if the relationship between muscle activation and end-effector force is known and assuming that the CNS minimizes some measure of effort, such as the sum of the square of muscle or synergy activity. Then, if individual muscles are activated flexibly and the force they generate is affected by noise whose variance increases with the level of activation (signal-dependent noise [2]), the planar force generated in the direction of action of an individual muscle must show a covariance ellipse elongated in the direction of the force. In contrast, if muscles are recruited within fixed synergies, for all force directions multiple muscles are activated simultaneously and the force covariance must be on average less elongated in the direction of the target force. For isometric forces generated by the index finger on a plane, the observed force covariance directness was found more compatible with a flexible than a synergistic model [3]. However, while the force covariance predictions depend on the estimation of the directional dependence of the muscle activation, a direct comparison of muscle tuning curve observed experimentally and those predicted by the
synergistic and flexible model has not been conducted.

In this study we have performed a comparison between the directional tuning of the activation of several muscles, acting on the shoulder and elbow joints, observed during the generation of planar isometric force at the hand and the tuning predicted by either a flexible or a synergistic model of muscle activation. These predictions require an estimation of the end-point isometric force generated by each muscle, which we assumed adequately approximated by a linear relationship between rectified and filtered EMGs and force, and an assumption of minimum effort muscle or synergy activation strategy. In addition, we have identified the muscle synergies underlying the generation of isometric hand forces using a non-negative matrix decomposition algorithm [25, 26], as in many recent studies.

II. METHODS

A. Experimental Procedures

We recorded surface electromyographic (EMG) activity from 13 muscles acting on the shoulder and elbow and isometric force applied by the arm in different directions in the horizontal plane. Five right-handed subjects (2 males and 3 females, 27 ± 3 years old) participated in the experiments after giving written informed consent. All procedures were approved by the Ethical Review Board of the Santa Lucia Foundation.

![Fig. 1 Experimental setup. Subjects sat in front of a desktop and inserted their forearm, wrist, and hand in a splint attached (inset) to a force transducer. A flat monitor occluded the hand and displayed a virtual scene matching the subject’s desktop view.](image)

Subjects sat on a racing car seat with their torso immobilized by safety belts anchored behind the shoulders and the hips and inserted their right hand and forearm in a splint, immobilizing hand, wrist, and forearm. A steel bar in the splint was attached with a steel rod to a force transducer positioned on a desktop in front of them. In this posture the center of the palm was aligned with the body midline at the height of the sternum and the elbow was flexed approximately by 90°. The height of the desktop and the distance of the chair from the desktop could be adjusted according to the subject’s size.

The subject’s view of the actual hand was occluded by a 21-inch LCD monitor positioned in front of the transducer and inclined so that the monitor surface was approximately perpendicular to the subject’s line of sight when looking at her or his hand (Fig. 1). The position of the subject’s eyes and monitor was estimated at the beginning of each experimental session with a calibration procedure based on aligning five horizontal lines positioned behind the monitor with corresponding lines displayed on the monitor. In this way, it was possible during the experiments to display on the monitor a virtual scene with a desktop matching the position and the wooden texture of the real desktop.

Subjects were instructed to apply forces on the horizontal plane. Force targets were shown as transparent gray spheres with centers on a horizontal plane at a height from the desktop surface matching the height of the subject’s palm. Force feedback was provided by the displacement, on the same horizontal plane, of a spherical blue cursor. The motion of the cursor was simulated in real-time as a critically damped mass-spring-damper system, i.e., according to \( m \ddot{x} + b \dot{x} + kx = F \), where \( x \) is the position of the cursor with respect to the center of the palm, \( F \) the recorded force, \( k \) is selected so that all force targets can be displayed on the screen, and \( b = 2 \sqrt{mk} \). The virtual scene was rendered using a dedicated PC workstation using custom software. The scene was updated at 60 Hz with the cursor position information processed by a dedicated data-acquisition PC workstation running a real-time operating system and transmitted through an Ethernet link using the UDP protocol.

At the beginning of each experimental session the mean maximum voluntary force (MVF) generated along 8 equally spaced directions in the plane was estimated and used to scale the magnitude of the force targets used in the rest of the session. Subjects performed then a series of 144 trials generating forces in 16 equally spaced directions (starting from 0°, lateral direction, in increments of 22.5°) and with 3 different magnitudes (0.1, 0.2, and 0.3 of the MVF) 3 times in each conditions in a randomized order. These force targets were selected to characterize the relationship between EMG and force across directions and in a range of magnitudes for which a linear approximation is adequate [27]. As the MVF was only used to equalize the magnitude of force targets across subjects, it was estimated along only 8 direction to minimize fatigue. At the beginning of each trial the subjects were instructed not to apply force and to maintain the cursor for 1 s within a transparent yellow sphere aligned with the center of their palm (rest phase). Then, a target gray transparent sphere appeared in one of 16 direction and 3 distances and subjects were instructed to reach it by applying forces in the target direction. The target sphere, which had a radius larger than the cursor sphere radius by 2% of the MVF, turned yellow when the cursor was inside it. Subjects were then required to maintain the cursor within the target for 3 s (hold phase) to successfully end the trial.

B. Data Collection

Forces and EMGs were recorded during each trial. Force and torques applied at the center of the palm were recorded
using a 6-axis transducer (Delta F/T Sensor, ATI Industrial Automation, Apex, NC, USA) but only the two horizontal planar components \(F_x\) (lateral direction – to the right of the hand–: \(F_y\) frontal direction – away from the chest) were used to displace the virtual sphere. Baseline force was measured while the subject was relaxed and subtracted. Surface EMG activity was recorded using active bipolar surface electrodes (DE 2.1, Delsys Inc., Boston, MA), band-pass filtered (20-450 Hz) and amplified (total gain 1000, Bagnoli-16, Delsys Inc.). Correct electrode placement was verified by observing the activation of each muscle during specific maneuvers [28]. The activity of the following 13 muscles was recorded and analyzed in this study: brachioradialis (BracRad), long head of biceps brachii (BicLong), short head of biceps brachii (BicShort), lateral head of triceps brachii (TriLat), long head of triceps brachii (TriLong), anterior deltoid (DeltA), middle deltoid (DeltM), posterior deltoid (DeltP), pectoralis major (PectMaj), teres major (TerMaj), latissimus dorsi (LatDorsi), infraspinatus (InfraSp), middle trapezius (TrapMid). Force and EMG data were sampled at 1 KHz using a A/D PCI board (PCI-6229, National Instruments, Austin, TX, USA) in the data-acquisition workstation.

C. Data Analysis

EMG data were used to characterize the directional tuning of muscle activations, to identify time-invariant muscle synergies, and, together with force data, to estimate a EMG-to-Force matrix.

1) Directional Tuning of Muscle Activations: EMG data were rectified and digitally low-pass filtered (2\(^{nd}\) order Butterworth, 5 Hz cutoff) and re-sampled at 100 Hz to reduce data size. In each trial, mean EMG activity of each muscle during the initial rest phase was used as an estimate of baseline noise level and subtracted from the rest of the data. Muscles and trials with noisy EMG signal (due to incomplete contact of the electrodes with the skin) were excluded from further analysis. In particular, BicShort was excluded in one subject (s1). Filtered EMG waveforms for each muscle were then time-averaged between 0.5 and 2.5 s during the 3 s hold phase and averaged across repetitions of the same condition (direction and magnitude) and normalized to the maximum activation across direction during MVF generation to construct, for each force magnitude, a directional tuning curve.

2) Muscle synergies: We then used a non-negative matrix factorization (NMF) algorithm [25, 26, 29] to decompose the vectors constructed with the filtered EMG activity of each muscle at each time sample \(m^k(t)\) during the hold phase of all trials \((k=1, \ldots, K)\), with \(K = 144\), 16 directions \(\times 3\) magnitudes \(\times 3\) repetitions). Thus, a data matrix \(M = [m^1(1), \ldots, m^K(T)]\) with 13 rows and 300 samples \(\times 144\) number of trials columns was created. Each vector (a column of the matrix \(M\)) was then reconstructed as the combination of a unique set of \(N\) vectors in muscle space, named time-invariant synergies \(\omega_i\) scaled by time-varying activation coefficients \(c_i(t)\)

\[
m(t) = \sum_{i=1}^{N} c_i(t) \omega_i
\]

or, equivalently, in matrix notation \(M = WC\), with \(W = [w_1, \ldots, w_N]\) and \(C = [c^1(1), \ldots, c^K(T)]\). For each \(N\) from 1 to the number of muscles, the extraction algorithm was repeated 5 times and the repetition with the highest reconstruction \(R^2\) was retained. The number of synergies \(N\) was then selected as (i) the smallest \(N\) for which the \(R^2\) was larger than 0.9 or (ii) the point at which the \(R^2\) vs. \(N\) curve had a change in slope (MSE error of linear fit from \(N\) to max(\(N\)) below \(10^{-4}\)), selecting the set with the smallest number of cases in which two synergies have a difference in preferred direction ([16] the direction of the maximum of the cosine function best approximate the directional tuning of the synergy coefficient) below 20º or above 160º.

3) EMG-to-Force matrix: The isometric end-point planar force (\(F\)) generated at the hand with the arm in a fixed posture (as both the trunk and the forearm were immobilized) by a muscle activation pattern \(m\) was modeled as linear combination of the end-point forces associated to each muscle: \(F = Hm\) where \(H\) is a matrix with dimensions \([2 \times M]\) (\(M\) number of muscles). For each subject we estimated such a matrix using multiple linear regression of each force component with the filtered EMG data recorded during the hold phase in all trials.

4) Model Prediction of Directional Tuning: We predicted the muscle pattern that either a flexible or a synergistic model of muscle activation would have generated for each force target used in the experiment according to the \(H\) (for both models) and the \(W\) (for the synergistic model only) matrices estimated from the data. As the goal was to investigate the synergistic organization of muscle patterns rather than other factors potentially affecting muscle activation, we made similar assumption on the optimization of the free variables of both models. We thus assumed that the muscle activations \((m^{\text{flex}}\) or \(m^{\text{syn}}\)) were selected by minimizing the sum of the square of the muscle or synergy activations for each force target \(F\)

\[
m^{\text{flex}} = \text{argmin}(\|m\|^2) \quad \text{with } F = Hm
\]

\[
m^{\text{syn}} = Wc^{\text{syn}} \quad \text{with } F = HWc
\]

We used the MATLAB function \texttt{quadprog} to find these minima, with non-negativity constraints on \(m\) and \(c\).

III. RESULTS

All subjects were able to reach the force targets presented randomly in 16 directions at a magnitude 0.1, 0.2, and 0.3 times their mean MVF and to maintain the force within the required 2% MVF tolerance for 3 s. An example of the raw EMG and force data collected is shown in Fig. 2 for a single trial in the negative x direction (i.e. to the left of the subject).
A. Directional Tuning of Observed Muscle Activations

As shown in previous studies [30], muscle activity was modulated by force direction and magnitude. Fig. 3 illustrates the directional and magnitude modulation of the activity of 13 arm muscles of subject 4. Some muscles showed a directional tuning resembling a cosine function (e.g. BicShort, DeltP, PectMaj, and InfraSp) and other muscles showed a broader and more complex tuning, sometimes with multiple peaks (e.g. TriLat, DeltM, and LatDors). These qualitative observations appear to be in contrast with a flexible model of muscle activation which predicts truncated cosine tuning [31, 32].

B. Muscle Synergies

We decomposed the muscle patterns recorded during the hold phase as combinations of muscle synergies using the NMF algorithm (see Methods). Fig. 4 shows 5 synergies identified in the muscle patterns of subject 4. Each synergy has a different balance of activation across muscles, with some muscle more strongly activated than others (BracRad and TeresMaj in W1, BicLong and BicShort in W2, LatDors in W3, TriLong in W4, and DeltP and InfraSp in W5) but with many muscles recruited in multiple synergies. Across subjects (Table I) the number of synergies selected (see Methods) ranged from 4 to 6 and the fraction of the total data variation explained by the synergies ($R^2$) ranged from 0.87 to 0.93. Thus, in accordance with a recent study [33], a small number of synergies captured the modulation of activity in many arm muscles across directions and magnitudes of isometric force generated at the hand.

Table I

<table>
<thead>
<tr>
<th>Subject</th>
<th>$N$</th>
<th>$R^2$</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>4</td>
<td>0.93</td>
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<tr>
<td>2</td>
<td>6</td>
<td>0.91</td>
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<tr>
<td>3</td>
<td>4</td>
<td>0.89</td>
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<tr>
<td>4</td>
<td>5</td>
<td>0.87</td>
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<tr>
<td>5</td>
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<td>0.89</td>
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</table>

Fig. 3 Directional tuning of muscle activations recorded in subject 4. The radius of the dashed circle in each plot represents the fraction of the maximum muscle activation across directions indicated by the numeric value at the bottom right. Muscle activations for targets at different force magnitudes are shown in different colors. Data points are connected by a cubic spline interpolant in polar coordinates.

Fig. 4 Muscle synergies identified with NMF in subject 4. The bar plot in each column (color coded) shown the components of the synergy vector $w$, normalized to the maximum in each synergy.
C. EMG-to-Force Matrix

As in previous studies of muscle activation during isometric force production [11], we modeled the mapping between EMGs and end-point force linearly. For each subject, a EMG-to-Force matrix was estimated by multiple linear regression. Fig. 5 shows the column of such matrix (H) for subject 4. We also estimated the force associated to the activation of individual muscle synergies by multiplying the Emg-to-force matrix with the synergy matrix (W, Fig. 5 right).

Most muscles had an estimated end-point force direction compatible with their musculoskeletal geometry. For example, in Fig. 5, BracRad, a pure elbow flexor muscle, generated a force in the approximate direction of the projection of the shoulder on the horizontal plane and TriLat, an elbow extensor, in the opposite direction. However, a detailed musculoskeletal model would be required for precise estimation of the direction of force generation; the model should have at least 4 degrees-of-freedom (3 at the shoulder and 1 at the elbow) and possibly more as the shoulder was not completely immobilized by the straps.

D. Directional Tuning Predicted by Flexible and Synergistic Activation Models

For each subject, we compared the muscle activation observed in all force directions and magnitudes with those predicted by a flexible recruitment of individual muscles or muscle synergies. In most cases, the observed directional tuning was predicted better by the synergistic than the flexible model.

Fig. 6 shows the directional tuning for the force targets at 0.2 MVF of subject 4. The results of the comparison varied across muscles and force directions. When the observed tuning (blue) differed from a simple cosine (e.g. for BracRad, TriLat, DeltA, DeltM, LatDorsi, TrapMed), in most cases the synergistic model (red) captured the data better that the flexible model (black) because the former can generate a directional tuning with multiple peaks while the latter can only generate (truncated) cosine tuning functions. In fact, with the synergistic model each muscle can be recruited by more than one synergy and it can therefore contribute to the force generation in multiple directions. This implies that the synergistic model predicts a larger amount of co-contraction across direction that the flexible model but this level of co-contraction is closer to that observed experimentally. However, even for the muscles that were best captured by the synergistic model the reconstruction error varied across force directions. In addition, for some muscles the activation predicted by the flexible model was very low (e.g. BicLong, TriLong, DeltM, LatDorsi, TrapMid). Both these observations may indicate that the assumption of a minimum muscle or synergy coefficient activation strategy is not correct or that the estimation of the EMG-to-Force matrix is not accurate.

Across all five subjects and for all force magnitudes, we found that the mean squared error of the prediction was lower with the synergistic model (Table II).
IV. CONCLUSIONS

We compared the directional tuning of arm muscle activation observed during the generation of isometric forces at the hand with the tuning predicted by a model of flexible recruitment of individual muscles and a model of recruitment of muscle synergies identified from the data with NMF. We found that the synergistic model predicted the experimental data better than the flexible model supporting the hypothesis that the CNS employs combinations of muscle synergies to efficiently, even if not optimally, select the muscle activity patterns required to achieve a goal. However, this result depends on the specific approximations and assumptions introduced in the models and further work is required to validate them. In particular, the results depend on the estimation of a subject-specific EMG-to-Force matrix which was performed with multiple linear regression. Such estimation could be constrained by a priori information on the musculoskeletal geometry and physiological characteristics of the muscles.

REFERENCES