Modularity in the motor system: decomposition of muscle patterns as combinations of time-varying synergies

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Abstract

The question of whether the nervous system produces movement through the combination of a few discrete elements has long been central to the study of motor control. Muscle synergies, i.e. coordinated patterns of muscle activity, have been proposed as possible building blocks. Here we propose a model based on combinations of muscle synergies with a specific amplitude and temporal structure. Time-varying synergies provide a realistic basis for the decomposition of the complex patterns observed in natural behaviors. To extract time-varying synergies from simultaneous recording of EMG activity we developed an algorithm which extends existing non-negative matrix factorization techniques.

1 Introduction

In order to produce movement, every vertebrate has to coordinate the large number of degrees of freedom in the musculoskeletal apparatus. How this coordination is accomplished by the central nervous system is a long standing question in the study of motor control. According to one common proposal, this task might be simplified by a modular organization of the neural systems controlling movement [1, 2, 3, 4]. In this scheme, specific output modules would control different but overlapping sets of degrees of freedom, thereby decreasing the number of variables controlled by the nervous system. By activating different output modules simultaneously but independently, the system may achieve the flexibility necessary to control a variety of behaviors.

Several studies have sought evidence for such a modular controller by examining the patterns of muscle activity during movement, in particular looking for the presence of muscle synergies. A muscle synergy is a functional unit coordinating the activity of a number of muscles. The simplest model for such a unit would be the synchronous activation of a set of muscles with a specific activity balance, i.e. a vector in the muscle activity space. Using techniques such as the correlation between pairs of muscles, these studies have generally failed to provide strong evidence in support of such units. However, using a new analysis that allows for simultaneous combinations of more than one synergy, our group has recently provided evidence in support of this basic hypothesis of the neural control of movement.
We used a non-negative matrix factorization algorithm to examine the composition of muscle activation patterns in spinalized frogs [5, 6]. This algorithm, similarly to that developed independently by others [7], extracts a small number of non-negative factors which can be combined to reconstruct a set of high-dimensional data.

However, this analysis assumed that the muscle synergies consisted of a set of muscles which were activated synchronously. In examinations of complex behaviors produced by intact animals, it became clear that muscles within a putative synergy were often activated asynchronously. In these cases, although the temporal delay between muscles was nonzero, the dispersion around this delay was very small. These observations suggested that the basic units of motor production might involve not only a fixed coordination of relative muscle activation amplitudes, but also a coordination of relative muscle activation timings. We therefore have developed a new algorithm to factorize muscle activation patterns produced during movement into combinations of such time-varying muscle synergies.

2 Combinations of time-varying muscle synergies

We model the output of the neural controller as a linear combination of $N$ muscle patterns with a specific time course in the activity of each muscle. In discrete time, we can represent each pattern, or time-varying synergy, as a sequence of vectors $\mathbf{w}(t)$ in muscle activity space. The data set which we consider here consists of episodes of a given behavior, e.g. a set of jumps in different directions and distances, or a set of walking or swimming cycles. In a particular episode $s$, each synergy is scaled by an amplitude coefficient $c_{si}$ and time-shifted by a delay $t_{si}$. The sequence of muscle activity for that episode is then given by:

$$\mathbf{m}_s(t) = \sum_{i=1}^{N} c_{si} \mathbf{w}_i(t - t_{si})$$

(1)

Fig. 1 illustrates the model with an example of the construction of a muscle pattern by combinations of three synergies. Compared to the model based on combinations of synchronous muscle synergies this model has more parameters describing each synergy ($M \times T$ vs. $M$, with $M$ muscles and $T$ maximum number of time steps in a synergy) but less overall parameters. In fact, with synchronous synergies there is a combination coefficient for each time step and each synergy, whereas with time-varying synergies there are only two parameters ($c_{si}$ and $t_{si}$) for each episode and each synergy.

3 Iterative minimization of the reconstruction error

For a given set of episodes, we search for the set of $N$ non-negative time-varying synergies $\{\mathbf{W}_i\}_{i=1,...,N}$, $\mathbf{W}_i = [\mathbf{w}_i(0) \ldots \mathbf{w}_i(T - 1)]$, of maximum duration $T$ time steps and the set of coefficients $c_{is}(\geq 0)$ and $t_{is}$ that minimize the reconstruction error

$$E^2 = \sum_{s} E_s^2$$

$$E_s^2 = \sum_{t=1}^{T_s} \left\|\mathbf{m}_s(t) - \sum_{i=1}^{N} c_{si} \mathbf{w}_i(t - t_{si})\right\|^2$$

The non-negativity constraint arises naturally in the context of motor control from the fact that firing rates of motoneurons, and consequently muscle activities, cannot be negative. While it is conceivable that a negative contribution on a motoneuronal pool from one factor would always be cancelled by a larger positive contribution from other factors, we chose a model based on non-negative factors to ensure that each factor could be independently activated.