Motor Control: Theories, Experiments, and Applications

Frederic Danion, PhD and Mark Latash, PhD

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CHAPTER

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5 Decomposing Muscle Activity in Motor TasksMethods and Interpretation

Lena H. Ting, Stacie A. Chvatal

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Abstract

This chapter examines methodologies for dimensional analysis and linear decomposition of multivariate data sets, and discusses their implicit hypotheses and interpretations for muscle coordination of movement. It presents tutorials to compare how two common methods—principal components analysis (PCA) and non-negative matrix factorization (NMF)—decompose electromyographic signals into underlying components. To facilitate the integration of such mathematical techniques with physiological hypothesis testing, the chapter focuses on developing an intuitive understanding to the two techniques. It provides a simple two-dimensional tutorial, focusing on how orthogonality constraints in PCA and non-negativity constraints in NMF impact the resulting data decomposition and physiological relevance. Examples are presented using real data sets from human balance control and locomotion. The chapter examines the structure of the resulting components, their robustness across tasks, and their implications for various muscle synergy hypotheses. The chapter addresses practical issues and caveats in organizing datasets, the selection of the appropriate number of components, and considerations and pitfalls of experimental design and analysis, as well as offering suggestions and cautions for interpreting results. Based on these comparisons and on the work in the visual system over the last decade, evidence is presented for the increased neurophysiological relevance of the factors derived from NMF compared to PCA.

Keywords: dimensional analysis, linear decomposition, multivariate data sets, muscle coordination, movement, principle components analysis, non-negative matrix factorization, data decomposition

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How do humans and animals move so elegantly through unpredictable and dynamic environments? Why does this question continue to pose such a challenge? During any motor task, many physiological elements throughout the body must be coordinated, such as limbs, muscles, neurons, etc. A major question in motor

control is: How do the overall functions and characteristics of movements arise from the functional arrangement and coordination of both neuromuscular elements and environmental interactions? Although modern technology allows us to collect an unprecedented amount of data on the activity of neurons, muscles, and limbs during a wide variety of behaviors, we still lack an understanding of how individual elements of the body interact to produce the many movements we perform, let alone characteristics such as grace or clumsiness.

Interpreting both structure and variability in the motor system and relating it to the resulting biomechanical and behavioral outputs remains a grand challenge in understanding how we move. Nikolai Bernstein noted the fact that motor behaviors never repeat themselves exactly, even when the same task is performed in succession (Bernstein 1967). On the other hand, he also noted that characteristic output patterns occur even when a motor task is performed by different sets of muscles, such as when drawing shapes or letters on a piece of paper versus on a blackboard, or with a different appendage. Similarly, more recent studies also demonstrate that the performance of a motor task, such as reaching to a target, can occur quite consistently even when there is a great deal of variability in the underlying joint motions or torques contributing to that task (Newell and Carlton 1988; Latash et al. 2002; Ko et al. 2003; Reisman and Scholz 2006). These findings highlight the fact that our bodies have a large number of degrees of freedom in the joints, muscles, and neurons that allow them to be flexible and functionally reconfigured to perform the same task, as well as different ↳ tasks (see Kelso, Sternad, this volume). During any so-called coordinated movement, synchrony and similarity are observed across many different kinematic, kinetic, electromyographic, and neural signals (Bernstein 1967; Macpherson 1991). But, when looking across a wide behavioral repertoire, the synchrony and coordination observed in one movement may be abolished in another, such that fluctuations in the spatiotemporal dynamics of the multiple measures may appear coordinated in one instance and independent in another (Bernstein 1967; Macpherson 1991). Such differences are potentially due to both changes in the neural control of muscles, as well as to changing interactions of the body with the environment under various conditions.

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Controlling movements requires not only organizing physiological processes for movement, but also requires consideration of the complex interactions of forces acting between the organism and the environment. Bernstein defined the coordination of movement as: "the process of mastering redundant degrees of freedom of the moving organ, in other words, its conversion to a controllable system" (Bernstein 1967). By "controllable" Bernstein meant that coordinated motor activity causes predictable biomechanical events, such as force generation and motion, that allow us to reliably perform a motor task. Thus, understanding movement requires characterizing the degrees of freedom of the physiological system that are used in the performance of any particular movement, the reconfiguration of such degrees of freedom in the performance of divergent movements (see Latash, this volume), and the relationships of these degrees of freedom to the biomechanical interactions that ultimately generate the movement (see Prilutsky, this volume). Gathering large sets of data during natural movements is becoming increasingly easier, thus allowing us to characterize coordination across many variables at different levels of the motor system; however, interpreting such large data sets and analyzing them to test motor control hypotheses remains a challenge.

Computational methods for analyzing large sets of data are now easily accessible and available; however, the utility of such methods for providing insight into motor control is debated. Can such techniques help us to understand increasingly large data sets? Can quantitative analysis provide further insight than that which scientists have gathered from observation? Are automated pattern-recognition techniques able to reveal that which an experienced scientist can see when examining raw data? What are the potential benefits and pitfalls of using such techniques? These questions will be addressed in this chapter.

Here, our goal is to provide instructive tutorials to provide an intuitive guide to the similarities and differences between two primary techniques used for the analysis and decomposition of multiple signals in

motor control and neuroscience, as well as in engineering fields: principal components analysis (PCA) and non-negative matrix factorization (NMF) (Lee and Seung 1999). Although comprehensive texts on the
p. 104 quantitative aspects ↳ of these techniques are readily available (Ramsay and Silverman 2005), we present methods for understanding how the properties of each technique affect the decomposition and physiological interpretation of muscle activation patterns in a simple example and in actual data from postural control and walking. We have chosen two commonly used linear decomposition techniques that render the most divergent results; however, similar principles could be used as a basis for comparing other decomposition techniques, such as independent components analysis (ICA) or k-means analysis (Tresch et al. 2006). We will discuss the interpretations and implications of the results and how such techniques might be used to understand principles of motor coordination, as well as give insight into the function of the nervous system in translating goal-level intentions into specific muscle activation patterns for movement.

Basic Properties and Differences Between PCA and NMF: A Simple Example

Although PCA and NMF are similar in their underlying concept and mathematical representations, there are key differences in their implementation and in the resulting components. Both PCA and NMF are linear decomposition techniques that assume that the set of measured data is composed of linear combinations of a smaller number of underlying elements (Fig. 5.1A). That is, given a number of simultaneous observations of multiple data channels, any particular observation could be represented as:

$$M_j = c_{1j}W_1 + c_{2j}W_2 + \ldots + c_{nj}W_n + \text{error} \quad \text{(Eq. 1)}$$

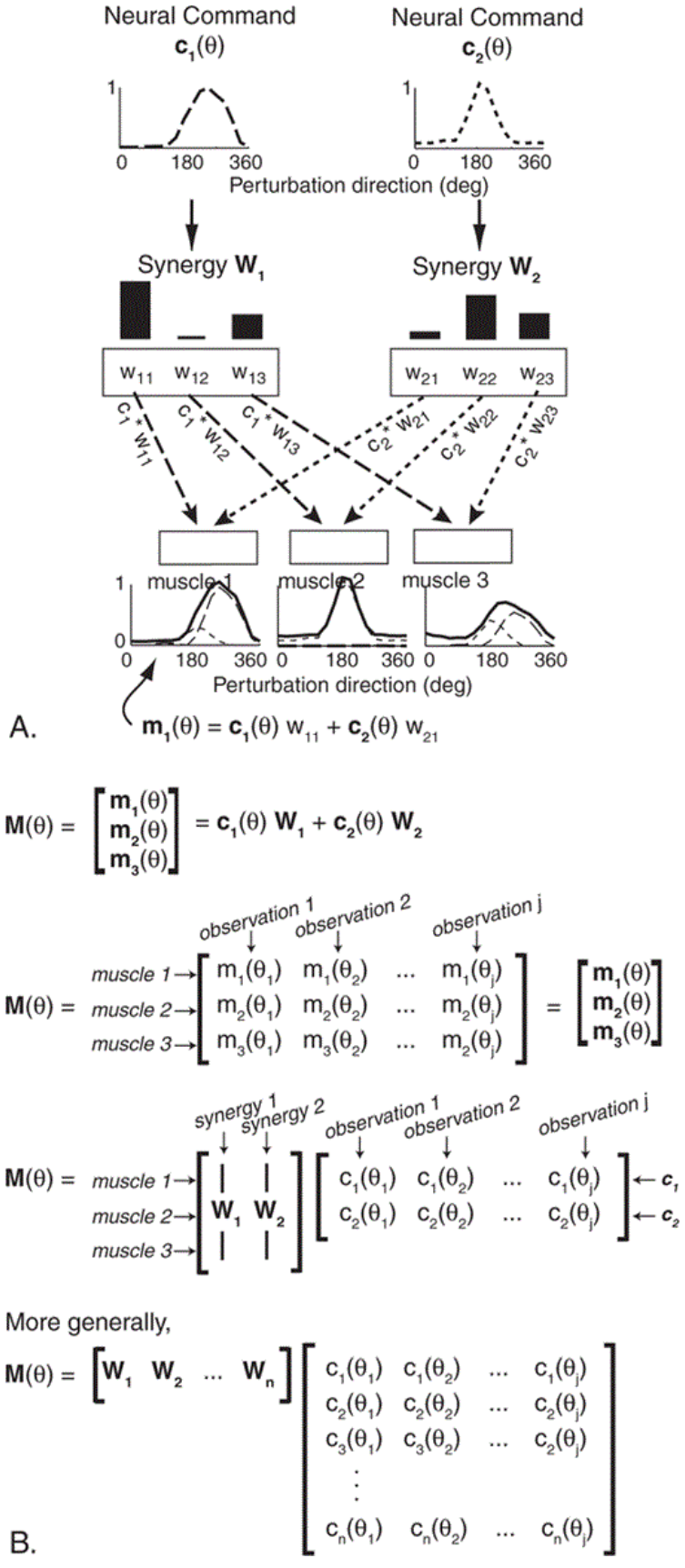

Figure 5.1 Electromyography (EMG) data decomposition schematic and muscle synergy concept. **A**: Any pattern of multiple muscle activation can be represented as a linear combination of the activations of that muscle by each muscle synergy component. In this example, there are $n = 2$ components and $m = 3$ muscles, thus $M(\theta)$ can be represented in terms of the lower-

dimensional combination of muscle synergies (components, W_i) and activation commands ($c_i(\theta)$). B) Organization of the data matrix and the structure of the W and c matrices.

Here, M_j is a vector that represents measurements of multiple channels of data (Fig. 5.1B); for example, the activity of *m* muscles at a given time point, arranged in a column. On the right side of the equation, the components or basis functions W_i are vectors, also of length *m*, that represent invariant patterns of activity across those different channels. The pattern of muscle activity can be described by *n* scalar values c_{ij}, each of which specifies the contributions of each component to the measured muscle activation pattern M_j. If there are *m* muscles and $n\langle m$ components, then the representation of M_j in terms of the components W_i and the weight or scaling factors c_{ij} is lower-dimensional than simply stating the value of each element of M_j. Such linear decomposition techniques therefore test the hypothesis that, over a large number of observations of M_j, the components W_i remain fixed, but the scaling factors c_{ij} are allowed to change and are sufficient to account for all of the variations of the data measured across different conditions. When analyzing muscle activation patterns, the modules W_i are often referred to as muscle synergies (Tresch et al. 1999; Cheung et al. 2005; Ting and Macpherson 2005; Torres-Oviedo and Ting 2007) or M-modes (Danion et al. 2003;
p. 105 Krishnamoorthy et al. 2004; Latash et al. 2007). In this context, the hypothesis ↳

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is that muscle synergies remain fixed, but activation of these synergies can vary, resulting in observed variations in individual muscle activity.

Although similar in concept, in practice, PCA and NMF are quite different; each method decomposes the variability within a given data set in very different ways. PCA is an analytical technique, meaning that the components are found through a straightforward set of computations. Therefore, it is easy to use and there are readily available algorithms included in most data processing software packages. This is possible because PCA requires that the components be orthogonal (e.g., perpendicular) to each other, creating a unique solution to any decomposition. Furthermore, it is relatively straightforward to select the appropriate number of components needed to explain a given data set based on a cutoff value for the variance accounted for. In contrast, NMF is found using a search algorithm, which means that it has to start with a set of random components and iteratively improve on them until an adequate proportion of the variability in the dataset is accounted for. Components generated by repeated searches will not be numerically identical but will be similar. Because NMF constrains both the weights c_i, as well as all of the elements of the components W_i to be non-negative, the problem is what is called *convex*. That is, there are no local minima for the search to be "stuck" in, therefore components from multiple searches are numerically similar. In a non-negative space, it is not possible for the components to be orthogonal; however, they must be independent, meaning that no component can be defined as a linear combination of the other components. The iterative technique also requires that the number of components be specified in advance, so that multiple searches must be done to determine the right number.

In the following set of tutorials, we use a simple two-dimensional example of a simulated dataset to illustrate the differences in how PCA and NMF decompose variability in the dataset. For all three examples, simulated muscle activity data are fabricated by assuming that there are two underlying components, which can be interpreted as muscle synergies, W_1 and W_2 that each define a different ratio between the activity of two muscles (Fig. 5.2A, *gray bars*). These components can also be drawn as vectors on a two-dimensional plot (Fig. 5.2A, *gray arrows*). A set of data, M, is created by randomly assigning the activation level of each component (c_1 and c_2) from a uniform distribution between 0 and 1. Each data point, or observation M_j, can
p. 107 be represented as a vector $[m_{1j}m_{2j}]$, and plotted as a single point on a set ↳ of axes representing the level of activation of muscle 1 versus muscle 2 (Fig. 5.2A). The tutorials are available for download as part of the supplementary materials, at http://neuro.gatech.edu/groups/ting/PMCtutorial.html.

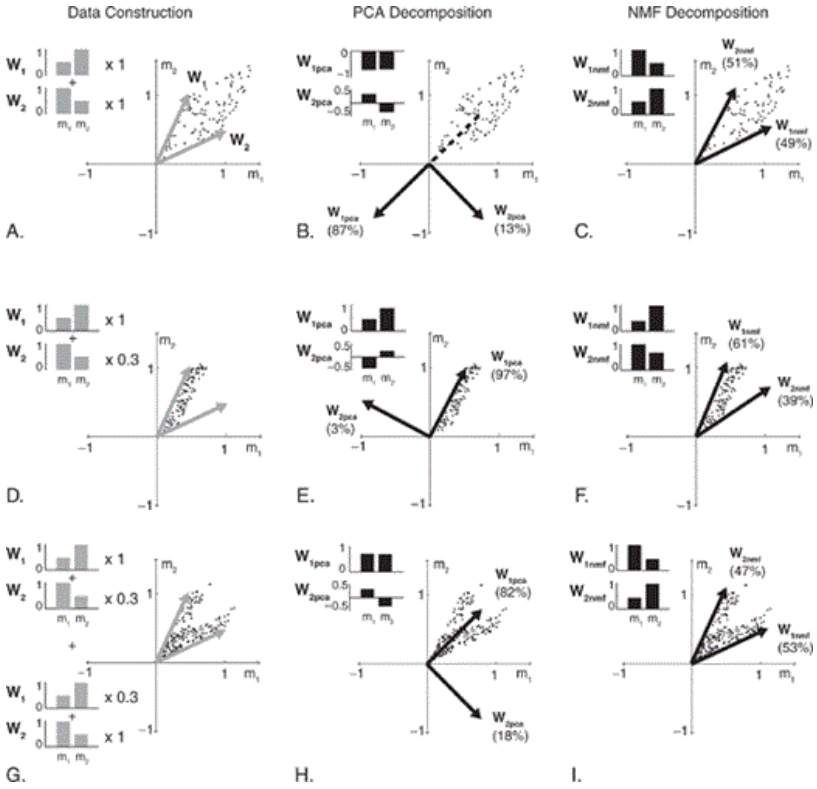

Figure 5.2 A 2-D example illustrating differences between components identified using principal components analysis (PCA) and non-negative matrix factorization (NMF). **A**: Data is constructed using two components specifying fixed ratios of muscle activation between two muscles, W_1 (m_1=0.5*m_2) and W_2 (m_1=2*m_2). The contribution of each component for a given observation, or data point, is found by multiplying each component by a scaling factor (c_1 and c_2) selected from a uniform distribution ranging from 0–1. **B**: Components identified using PCA to decompose the data from A. The percentage of total data variability that each component accounts for is shown beside each vector. The first component is directed along the long axis of the data cloud, and the second is constrained to be in the orthogonal direction. C: Components identified using NMF to decompose the data from A. Components are found near the edges of the data cloud. Note the similarity to the original components (W_1 and W_2) used to generate the data. **D**: Data is constructed using the same two components as in A, except now it is weighted towards using W_1. In order to generate this data, $\mathbf{c}_1$ was taken from a uniform distribution between 0 and 1, whereas $\mathbf{c}_2$ was taken from a uniform distribution between 0 and 0.3. **E**: Components identified using PCA to decompose the data from D. W_{1pca} looks similar to W_1, reflecting the bias towards W_1 in the generation of the data set, but W_{2pca} is different from W_2. **F**: Components identified using NMF to decompose the data from D. Despite the bias in the generation of the data set, these components are similar to those used to generate the data, as well as the components identified in C. **G**: Data is constructed using the same two components as in A and D, except now part of the data is weighted towards using W_1 and part is weighted towards using W_2. To generate this data, c_1 was taken from a uniform distribution between 0 and 0.3, whereas c_2 was taken from a uniform distribution between 0 and 1, and this was included along with the data from D. **H**: Components identified using PCA to decompose the data from G. W_{1pca} passes between the two "clouds" of data where the mean values of m_1 and m_2 lie, and the components look similar to those identified in B. **I**: Components identified using NMF to decompose the data from G. Again the components are similar to those used to generate the data.

Orthogonality Versus Independence

The constraints of orthogonality and independence in PCA, and independence without orthogonality in NMF, account for the large differences between the components extracted by each technique. In this example, the activity of each component was equally weighted, so that the data is scattered evenly between the two vectors, W_1 and W_2, used to create the data (Fig. 5.2A). When PCA is applied to the data, two components are extracted (Fig. 5.2B). The first aligns with the center of the long axis of the data and accounts for 87% of the variability. Because the scaling factors can be positive or negative, the direction that W_1 points does not matter, only the line it defines. The second component must be at a right angle to the first component to satisfy orthogonality. It accounts for a much smaller portion of the variability, only 13%. Neither PCA component looks like the original components used to generate the data. Using NMF, the extracted components are similar to the original components, W_1 and W_2, used to generate the data, appearing at the edges of the data points (Fig. 5.2C). The variability accounted for by each component is similar, 49% and 51%, respectively. Although the components are not orthogonal, the addition of a second component nonetheless increases the set of possible patterns of muscle activation between muscles 1 and 2.

PCA Is Descriptive; NMF Is Prescriptive

PCA, much like a multiple regression, describes the mean and residual variance from the mean in successive principal components. Before identifying the components, the original dataset is typically demeaned; if this is not done, then the first principal component represents the mean value of each variable across the dataset. Otherwise, as in this example, the first principal component in PCA describes the largest deviation from that mean in each muscle across a given dataset. Each additional component describes the orthogonal direction containing the next largest deviations from that mean. In our two-dimensional example, it means that if the first component changes, then the second component must also change. The percentage of variability accounted for by each component decreases monotonically, describing the degree to which the dataset varies in the corresponding direction. Because PCA allows for both negative and positive values for the scaling factors, it is possible to describe any point on the plane with two independent components derived from data in that plane, regardless of the direction that they point (Fig. 5.2B). Data with multiple
p. 108 dimensions can be restricted to a plane by choosing only the first two principal components. ↳

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p. 110 In NMF, the components prescribe a subspace within which all data points must lie. Because of the non-negativity constraints, only the points lying between the two components can be described (e.g., Fig. 5.2A). Thus, components from NMF tend to identify the edges of the dataset and define a convex hull, or polygon, within which all of the feasible data points lie (e.g., Fig. 5.2C). The condition of independence requires that each additional component increase the allowable subspace, as no two components can be represented as a linear combination of other components. Because there is no constraint on orthogonality, it is also possible for one component to change and the others to remain the same.

Therefore, the non-negativity constraints within NMF make it more restrictive than PCA, delimiting regions of the low-dimensional space that cannot be reached. Although dimension reduction can be achieved in both techniques by examining only the first few components, NMF imposes further restrictions. Components derived from PCA tend to *describe* the major direction of the data without imposing restrictions within the space defined by those components. In contrast, NMF *prescribes* a subspace in which possible combinations of muscle activity lie, restricting the expressible data points using those components.

Consider an example using the same components, W_1 and W_2, as in the previous tutorial, except this time the data are preferentially weighted toward using W_1 (Fig. 5.2D, data construction). This dataset was created from sampling the same muscle activation components as in the prior example, but with a higher activation

of W_1 over W_2. Using PCA, both components changed direction compared to the previous tutorial (compare Fig. 5.2E and 2B). The first PCA component (W_{1pca}) rotated closer to the mean of the observed pattern of muscle activity and now looks qualitatively similar to the original W_1 used to construct the data (Fig. 5.2A), accounting for 97% of the variance. The second component must rotate a similar amount to maintain orthogonality (compare Fig. 5.2B and 2E). Both components identified in this case look different from those identified using PCA in the previous example. Thus, PCA describes the data in a similar sense to a mean and standard deviation. In contrast, both components found using NMF (Fig. 5.2F) were similar to the components W_1 and W_2 used to generate the data (Fig. 5.2D) and to those identified in the previous tutorial (Fig. 5.2C). There was a slight shift in the second component simply because there is less variance in that direction, and therefore a larger confidence interval. Thus, the components obtained from NMF identify vectors that prescribe the same space of possible solutions using those two components as in the prior tutorial, even when one component is more heavily weighted than the other.

Physiological Interpretability of PCA Versus NMF Components

In PCA, a component, $W_{i,}$ can contain positive and negative numbers representing relative muscle activation
p. 111 levels, as well as positive and negative ↳ weightings, c_i. This means that positive and negative relationships can be inverted easily by negative weighting values. In the context of muscle activation patterns, this equal relationship between positive and negative activation is inconsistent with the transformation between motorneuron action potentials and muscle activity. Although motoneurons no doubt receive inhibitory as well as excitatory neural activity, the inhibitory effect can only be seen on motor output if there is also a high background level of muscle activity. That is, if inhibition occurs when muscles are quiescent, they have no effect on muscle activity due to the rectifying properties of neural transmission. Moreover, excitatory pathways and effects cannot be made inhibitory, and vice versa, so that there is no reason to think that an excitatory pattern would be identical to an inhibitory one. In contrast, in NMF, the components are constrained to be non-negative, which is physiological for neural and muscle output, since neurons are either firing action potentials (positive signal) or else in a resting state (zero signal).

One interesting result of the non-negativity constraint in NMF is that the underlying components resemble a "parts-based" decomposition, in which a series of parts are summed to create a whole. Since each component, or part, that is added cannot be subtracted out through the contributions of another component, the parts must resemble identifiable features of the output. In contrast, allowing negative numbers in PCA means that a given data point is created by addition and subtraction of contributions from different components to a given muscle's activity. The first component describes the mean, and the next components can add or subtract activity from that mean. Therefore, the resulting data point may bear no resemblance to the identified principal components.

Here, we demonstrate the different ways in which PCA and NMF deal with data that are not evenly distributed. Consider an example using data constructed from the same components, W_1 and W_2, from the first two tutorials, except now part of the data is skewed toward using W_1 and part skewed toward using W_2 (Fig. 5.2G). The components identified using PCA are similar to those found in the first tutorial: The first component passes between the two main "clouds" of data, and the second is orthogonal to the first (compare Fig. 5.2H to 2B). In contrast, components extracted using NMF look very similar to the original $W_1$and W_2 used to generate the data, as well as to those identified in the first two tutorials (compare Fig. 5.2I to 2F and 2C). The components lie along the edges of the data "clouds," and therefore can be used to describe any data points between them.

In this example, the components from PCA are directed in similar directions as in first example, with the first component aligned along the mean values of m_1 and m_2 across the dataset (Fig. 5.2H). Most of the data points are reached by scaling the contribution of the first component and adding or subtracting a

contribution of the second component. However, these components do not resemble the two-armed "parts" of the dataset. In contrast, the components from NMF are again similar to those used to generate
p. 112 the data, and similar to the components found from the two other ↳ data sets (Fig. 5.2I). Here, the two components from NMF clearly identify two of the underlying "parts" that are obvious in the dataset (similar results can also be achieved through independent components analysis [ICA] in combination with PCA [Hyvärinen 2001; Tresch et al. 2006]).

Similarly, in the original paper describing differences between PCA and NMF, the components underlying decomposition of an image of a face were compared (Lee and Seung 1999). All of the PCA components look like entire faces, which are then added and subtracted together to generate a given face. To generate a face with a medium nose, large eyes, and small mouth, one might imagine starting with the mean face expressed by the first principal component and adding a component with a large nose, large eyes, and medium mouth, then subtracting another component with a small nose, medium eyes, and small mouth. The NMF components, however, are characterized by face parts such as the nose, eyes, and mouth. A face would be generated by selecting a component nose, scaling it by a medium number, selecting a component eyes and scaling it by a larger number, and selecting a component mouth and scaling it by a smaller number. Interestingly, this kind of parts-based decomposition is similar to the type of neural representations observed in the visual and other sensory encoding systems (Olshausen and Field 2004). Accordingly, there has been a shift from the use of PCA to NMF in visual system research (Simoncelli and Olshausen 2001).

Identifying Components Using PCA and NMF: A Postural Control Example

Taken together, these three tutorials illustrate key differences in how PCA and NMF describe and partition the variability in a given data set, which are relevant to how they can be used to test motor control hypotheses. Although all of the data were generated from the same set of underlying components, the components identified by PCA changed when the mean levels of muscle activation changed, and all of the components changed simultaneously. NMF has the ability to identify components that are stable across different conditions, but combined differently. This demonstrates how different conclusions regarding the robustness and generality of components might be drawn depending on which decomposition algorithm is used.

In the literature, both PCA and NMF have been used to examine whether stable motor modules are used for generating movements. Several studies have addressed muscle coordination in standing balance control, because muscles in various regions of the body tend to act synchronously, and patterns of muscle activation can be easily related to a direction of body motion. During postural body sway, PCA has been used to identify components, called *M-modes*, that correspond to the direction of center of pressure changes used to stabilize the body (Aruin et al. 1998; Krishnamoorthy et al. 2003a). Similarly, in responses to different
p. 113 directions of perturbation during ↳ standing balance control, components from NMF, referred to as *muscle synergies*, have been identified that correspond to the direction of force applied at the ground to stabilize the body (Ting and Macpherson 2005; Torres-Oviedo et al.2006). However, as the number of postural conditions is increased, the underlying M-modes from PCA are found to change (Krishnamoorthy et al. 2004), whereas the muscle synergies from NMF remain consistent (Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2010).

Rarely are both techniques used in the same study, so that it is difficult to know whether the differences in the literature reflect the techniques used, the experimental design, or the particular motor tasks tested. Moreover, since NMF requires several decisions on the part of the investigator, choosing the right number of muscle synergies is not necessarily straightforward, which may also lead to different conclusions being

drawn. Here, we provide examples where both PCA and NMF are performed on actual data from one subject during postural responses to multidirectional perturbations.

Introduction to Postural Responses

In order to maintain balance in light of an unexpected perturbation of the support surface, humans and animals must keep the projection of their center of mass (CoM) within the limits of their base of support. Various strategies may be used when balance is disrupted, requiring the activation of different muscles, such as taking a step, grabbing a handrail, or maintaining the feet in place to restore balance. When standing balance is disturbed with a discrete perturbation, first the direction of falling is sensed, and then the appropriate muscles are activated to restore balance. The initial change in muscle activity in the lower limbs does not occur until approximately 100 ms following the onset of a perturbation, and this initial muscle activity is called the *automatic postural response* (APR). Variations are observed even in responses to the same perturbation direction due to attention, expectation, and the like (Woollacott and Shumway-Cook 2002). When many trials and many perturbation directions are examined, the differences observed in individual muscle activations are difficult to interpret (Horak and Macpherson 1996; Henry et al. 1998). One hypothesis is that the nervous system activates these muscles in groups, and decomposition techniques such as PCA and NMF can be used to identify such groups and the relationships between the muscle activations (Krishnamoorthy et al. 2003a; Krishnamoorthy et al. 2003b; Torres-Oviedo and Ting 2007).

To generate the postural data examined here, subjects stood on a platform, which was suddenly moved in one of 12 different directions in the horizontal plane. Electromyographic (EMG) signals were collected from 16 lower trunk and leg muscles from the right side. For each trial, mean muscle activity during three time windows during the APR was calculated: 100–175 ms following perturbation onset (PR1), 175–250 ms (PR2),
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250–325 ms (PR3), as well as one background time window before the perturbation began (Fig. 5.3A). Therefore, this data set consisted of 16 muscles and 240 conditions (4 time windows × 12 perturbation directions × 5 trials in each direction). All of the data were arranged in a matrix in which each of the 16 rows contains the 240 observed values for a single muscle. The values in each row were normalized to the maximum value in that row, corresponding to the maximum level of muscle activity observed for that muscle across all conditions. Therefore, for each muscle all values ranged from 0 to 1. Before components are extracted using NMF, each muscle was also normalized to have unit variance, meaning that the sum of the squared values in the row equals 1. This allows the variations in each muscle to be considered with equal importance by the algorithm. One practical consideration is that, for NMF, the data should always be presented in the format N muscles × M conditions. However, PCA requires the data be transposed, in the format N conditions × M muscles.

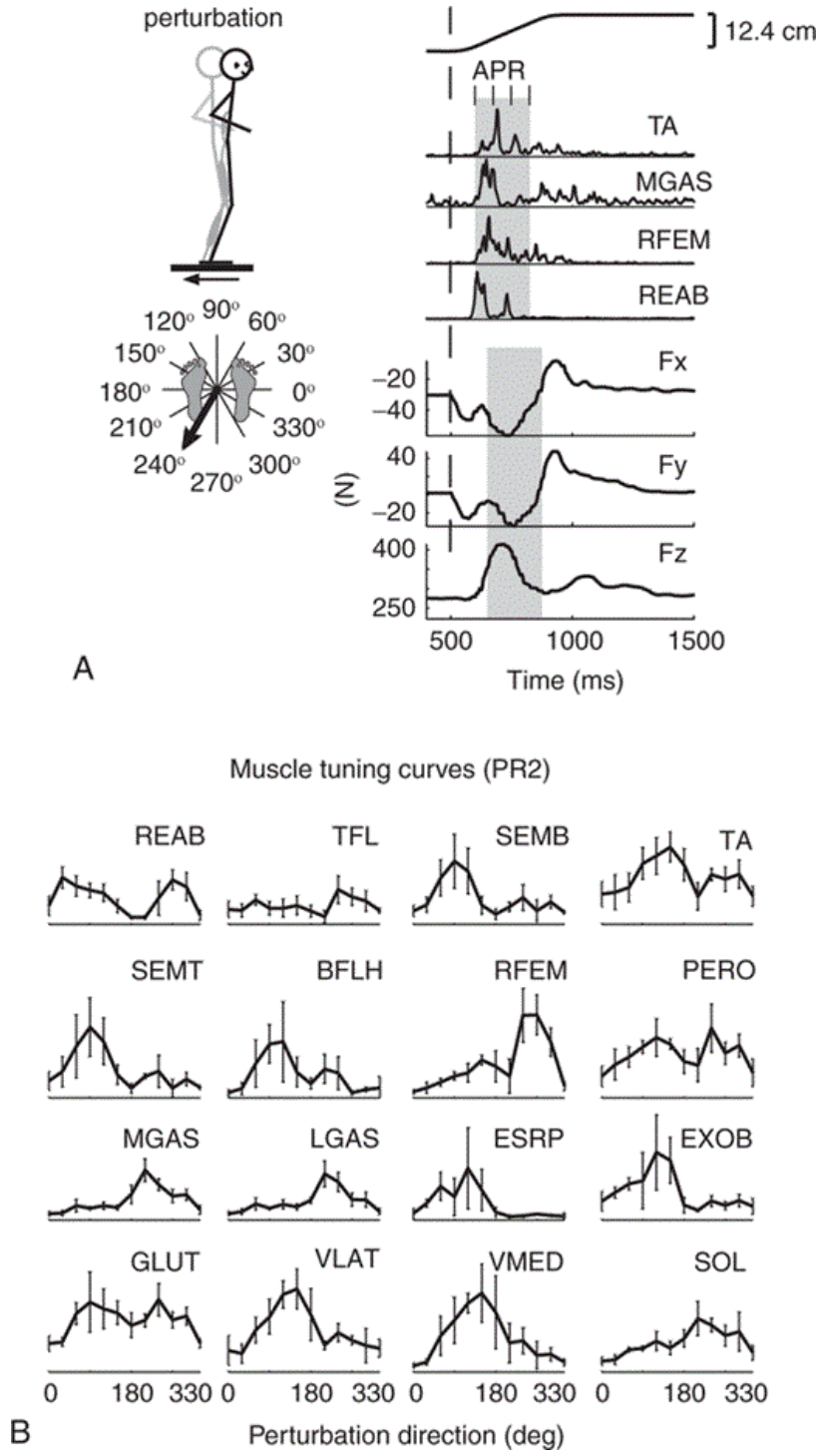

Figure 5.3 Example of postural responses to a backward and leftward perturbation of the support surface. **A**: Platform displacement during the ramp-and-hold perturbation. Electromyograph (EMG) responses occur 100 ms after the onset of platform motion (*vertical dashed line*). Shown here are tibialis anterior (TA), medial gastrocnemius (MGAS), rectus femoris (RFEM), and rectus abdominus (REAB) EMG responses. Mean EMG activity was calculated for three time bins during the APR (*shaded region*), beginning 100 ms (PR1), 175 ms (PR2), and 250 ms (PR3) following perturbation, as well as one background time period. Ground reaction forces under the right foot are also shown. **B**: Muscle tuning curves generated from 12 evenly spaced perturbation directions, taken from time window PR2. Muscle tuning curves vary in magnitude over all perturbation directions, and their shapes vary from muscle to muscle. In addition to the four muscles shown in A, tensor fasciae latae (TFL), semimembranosus (SEMB), semitendinosus (SEMT), biceps femoris long head (BFLH), peroneus (PERO), lateral gastrocnemius (LGAS), erector spinae (ERSP), abdominal external oblique (EXOB), gluteus medius (GLUT), vastuslateralis (VLAT), vastusmedialis

(VMED), and soleus (SOL) were also collected. Shown are the mean tuning curves ± standard deviations for five trials in each perturbation direction, presented randomly.

In response to horizontal plane disturbances, each muscle was preferentially activated for particular perturbation directions (Fig. 5.3B). The muscle "tuning curves" demonstrate the directional sensitivity of the muscles. Each muscle is active maximally in a given direction, and less so for other directions. Some muscles have a single preferred direction (e.g., vastusmedialis, VMED), whereas others have multiple tuning directions (e.g., rectus abdominus, REAB). The muscle tuning curves demonstrate that each direction of perturbation evokes a different combination of muscle activity. The error bars on the muscle tuning curves also illustrate trial-to-trial variations observed in postural responses. Therefore, across perturbation directions, and even within a perturbation direction, different patterns of muscle activity are evoked. Does this mean that each muscle must have an independent neural command specifying its level of activation (Macpherson 1991)? Using NMF and PCA, we can test the hypothesis that the observed variations can be explained by the activation of a few muscle synergies (Fig. 5.1). In the following section, we will compare how NMF and PCA describe postural response data, address practical issues of selecting the appropriate number of components, and examine the robustness of the components across different postural tasks,
p. 116 specifically, two-legged versus one-legged perturbation responses. ↳

p. 117 ## Components of Postural Responses Identified by PCA and NMF

Here, we compare five components selected by NMF and PCA to describe the postural response data for normal, two-legged stance (the procedure for selecting the number of components will be described in a later section).

The components identified by PCA are composed of muscle contributions that are both positive and negative, and are activated by weighting coefficients (or scaling factors) that may also be positive or negative (Fig. 5.4A). This example illustrates again that the components are identified in order of the percentage of variance that each explains. The first component describes the mean level of activity of the muscles across all conditions, and therefore has positive contributions from all of the measured muscles, with strong contributions from TA and PERO (Fig. 5.4A, W_{1pca}). The first component is also strongly activated for forward (90-degree) and backward (270-degree) perturbation directions, which evoke much more muscle activity than lateral perturbation (Henry et al. 1998). The subsequent components have contributions from fewer muscles, and these contributions are both positive and negative. Additionally, the activation coefficients may be positive or negative for different perturbation directions, and the magnitude of activation decreases with each subsequent component.

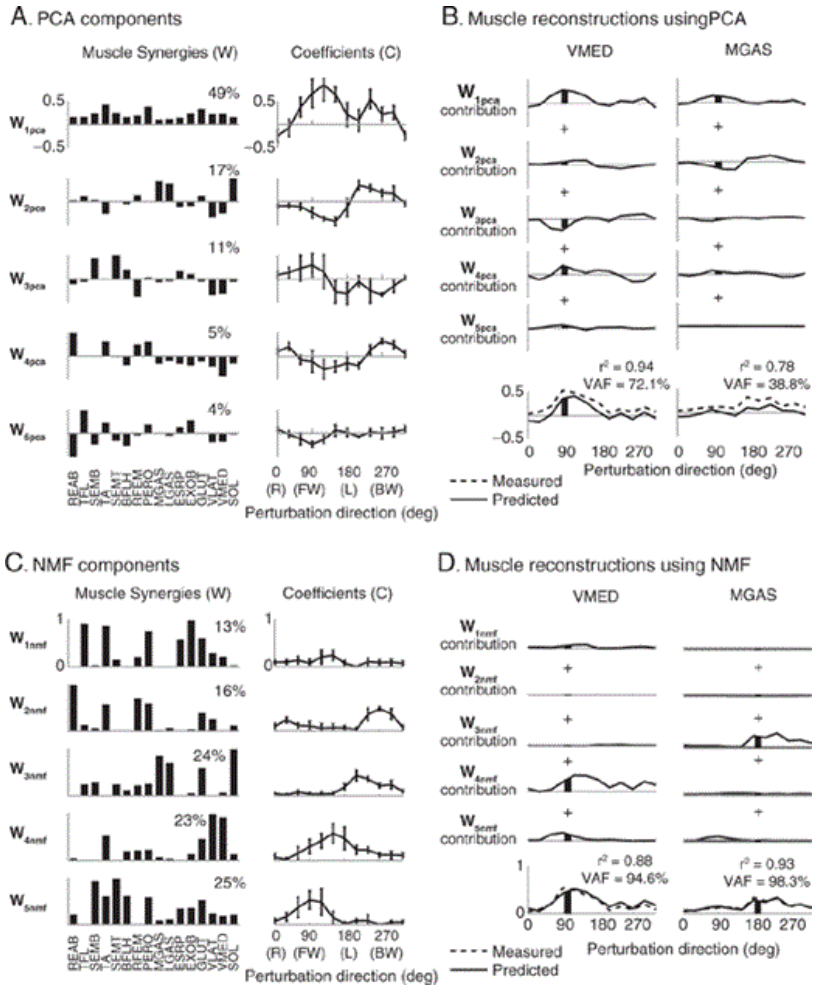

Figure 5.4 Components and activation coefficients identified from postural response data using principal components analysis (PCA) and non-negative matrix factorization (NMF). **A**: Components identified using PCA may have positive and/or negative muscle contributions and activation coefficients. Each bar represents the contribution of that muscle to that component. Percentages indicate the amount of total data variability accounted for by each component. Activation coefficient tuning curves from PR2 are shown as mean ± standard deviation of five trials. **B**: Tuning curves created from a single trial in each direction for two muscles reconstructed using the components identified in A. The contribution from each component is added or subtracted to form the reconstructed muscle tuning curve. The original data are shown with a dashed black line and the reconstructed data are shown with a solid black line. The variability accounted for (VAF) by the reconstruction as well as r^2 values are shown for each muscle tuning curve. **C**: Components identified using NMF have only positive muscle contributions and activation coefficients. Percentages indicate the amount of total data variability accounted for by each component. Activation coefficient tuning curves from PR2 are shown here as mean ± standard deviation of 5 trials. **D**: Two muscle tuning curves reconstructed using the components identified in C. The contribution from each component is added to form the reconstructed muscle tuning curve. The original data are shown with a dashed black line and the reconstructed data are shown with a solid black line. The variability accounted for (VAF) by the reconstruction as well as r^2 values are shown for each muscle tuning curve.

The way in which PCA decomposes data can best be illustrated by examining how the components contribute to an individual muscle tuning curve. Due to the positive and negative values taken both by the components and the activation coefficients in PCA, contributions from different components can be added and subtracted to obtain the total predicted muscle activity. An example of this can be seen in the reconstruction of the VMED tuning curve from the individual contributions from each component (Fig. 5.4B), which are found by multiplying the height of the VMED bar in each component with the activation coefficient for a given direction. Thus, each of the contributions resembles a scaled and possibly inverted version of the activation coefficient tuning curves of each component (Fig. 5.4A). The resulting tuning curve

for VMED is generated by adding all five curves together (Fig. 5.4B, *bottom*). Although the peaks of the various contributions can vary, the resulting VMED tuning curve peaks near 90 degrees, and is roughly zero between 180 and 360 degrees. The response ↳ of the VMED to the 90-degree perturbation is high, and is due to positive contributions from $W_{1pca,}$ W_{2pca}, W_{4pca}, and W_{5pca} and a negative contribution from W_{3pca} (Fig. 5.4B, *bars*). Similarly, in the region between 180 and 360 degrees, negative and positive contributions from all the components cancel each other out, so that the resulting tuning curve is near zero. To reconstruct the tuning curve of MGAS, the same curves are scaled differently and added together. The near-zero activity of MGAS in the 90-degree perturbation direction results from the cancellation of positive and negative contributions, primarily from W_{1pca} and W_{2pca}. In general, when using components identified by PCA, the reconstructions tend to underpredict the recorded muscle activity.

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In contrast to PCA, the components and activation coefficients identified by NMF contain only positive values, as constrained by the algorithm. They are identified in no particular order, as evidenced by the percentage of total variance accounted for by each component (Fig. 5.4C). Each component has large contributions from a few muscles, and smaller contributions from several other muscles, illustrating the multijoint coordination required for postural control. Each component has a corresponding activation coefficient that is tuned for a particular range of perturbation directions. These activations are also positive, and the magnitude of activation is similar across all five of the components.

The reconstruction of the individual muscle tuning curves illustrates the differences between PCA and NMF in the way the components are combined to predict the recorded data. As with PCA, the height of the VMED bar in each NMF component is used to scale the contribution of each component's tuning curve. In this case, since VMED is virtually zero in W_{2nmf} and W_{3nmf}, these components make essentially no contribution to the VMED tuning curve. In contrast to the case with PCA decomposition, the activity of VMED at 90 degrees is due to the additive contributions of three components W_{1nmf}, W_{4nmf}, and W_{5nmf} (Fig. 5.4D).

Using NMF, there is no cancellation of features (Fig. 5.4D). Each muscle's activity is reconstructed by adding the contributions from each muscle synergy, all of which are positive. Once a feature of the tuning curves is expressed in the contribution of a given component, it cannot be subtracted out. For MGAS, the tuning curve consists primarily of contributions from W_{3nmf}, which causes high activity of MGAS between 180 and 360 degrees, and W_{5nmf}, which is responsible for a low level of activity of MGAS between 0 and 180 degrees.

The separation of the contributions from each component makes it possible to use the patterns of muscle activity within each component to make predictions about the activity of other muscles. In this case, the activity of MGAS between 180 and 360 degrees can be attributed to W_{3nmf}, which coactivates high MGAS activity with high extensor activity in the LGAS, GLUT, and SOL. When MGAS is active between 0 and 90 degrees, its activity is due to W_{5nmf}, which coactivates small MGAS activity with high flexor and hamstring activity in SEMB, TA, and SEMT. This demonstrates that MGAS ↳ activity in different perturbation directions results from fundamentally different muscle coordination patterns. It may be a prime mover in 180- to 360-degree perturbations, and a stabilizer in 0- to 90-degree perturbations. The analysis demonstrated that MGAS is strictly covaried with SOL from 180 to 360 degrees, and strictly covaried with TA from 0 to 90 degrees. A traditional correlation analysis would reveal MGAS to be strongly correlated to SOL, and weakly correlated to TA, but it would not be able to decompose the different portions of MGAS activity to one or the other.

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Here, the coefficient of determination (r^2) and variability accounted for (VAF), which are measures of goodness-of-fit between the predicted and recorded EMG signals, demonstrate that NMF components can explain the recorded muscle responses more closely than PCA components (NMF average r^2 for all muscles: 0.84, average VAF: 95.5%; PCA average r^2 for all muscles: 0.81, average VAF: 58.9%). Both r^2 and VAF are defined as the coefficient of determination, or percent variability accounted for in the dataset (1 – sum of squares error/total sum of squares). The Pearson correlation coefficient, r, is based on a linear regression

with an offset and thus compares only shapes of two curves, allowing for their actual values to differ. VAF is based on a linear regression that must pass through the origin, and therefore requires that the actual values of the measurements be equal to have a high percent of variability accounted for. In the standard Pearson correlation coefficient (r^2), the sum of squares is taken with respect to the mean, whereas in the uncentered case (VAF), it is taken with respect to zero. In this postural example, PCA reconstructs the shape of the tuning curve well, but not the offset; as expressed by the reasonably high r^2 values, but much lower VAF. In contrast, NMF reconstructs the level of activity well, and allows for more differences in the shape of the curve, which is evidenced in the high VAF values.

Selecting the Appropriate Number of Components Using NMF

In both NMF and PCA, the investigator must determine the number of components required to sufficiently explain the data. With PCA, a cutoff of the total percent variability explained is typically chosen, and the components with the largest contributions are chosen to meet that criterion. A similar criterion can be used in NMF, in which the analysis is run multiple times, each with a different number of components, and VAF can be plotted as a function of component number (Fig. 5.5A). In this postural data example, a cutoff of 90% VAF selects four components. Note, however, that the VAF due to one component is very high, so that high VAF values can be misleading in the overall variability because generally they represent a small portion of the data having a large amplitude that contributes the most to the overall data variability.

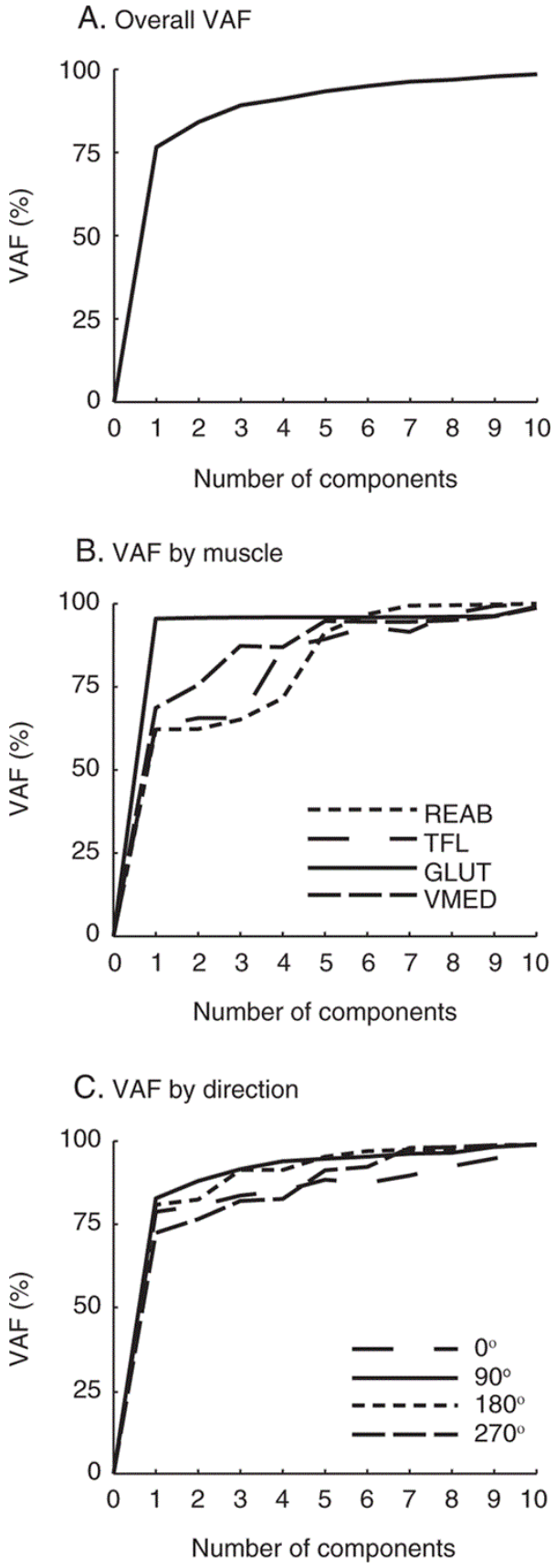

Figure 5.5 Scree plots showing variability accounted for (VAF) between the original data and the reconstruction using non-negative matrix factorization (NMF) components for the data shown in Figure 3. **A**: VAF for increasing number of components over the entire data set. **B**: VAF for increasing number of components for four individual muscles: REAB, TFL, GLUT, VMED. One component accounts for variability in GLUT relatively well, three components can explain VMED variability, but five is better at

explaining variability in TFL and REAB. **C**: VAF for increasing number of components across individual perturbation directions. Shown here are the four cardinal directions, but the number of components needed was selected by looking at these types of plots for all muscles and all perturbation directions.

Whether using PCA or NMF, using the overall variability accounted for to select the number of components
p. 120 may not generate adequate reconstructions of data, particularly when there are certain conditions in which
↳

p. 121 ↳
generally less activity occurs, but which nonetheless are an important feature of the dataset. In the postural control example, the overall level of muscle activity is higher in forward and backward directions. When choosing a smaller number of components, the muscle activity in forward and backward directions tends to be well-explained, whereas activity in lateral directions may not be well-reconstructed. Because muscle activity in lateral directions represents a small fraction of the total variability, it is difficult to discern from the overall VAF scree plot when such variations are accounted for. In both analyses, large differences in the magnitude of the variability across conditions always poses a problem when selecting components.

A number of additional criteria can be imposed to ensure that desired features of the dataset are reconstructed. For our postural control example, we further examined the variability accounted for within subsets of the data. We examined the VAF of each muscle, which ensures that each muscle's tuning curve is well-reconstructed. In certain cases, when a muscle's contribution to the overall variability is low, the features of its tuning curve may not be well reconstructed by the selected number of components, requiring additional components to be added. We then examined the data by perturbation direction, ensuring that the differences in the relative levels of activity by direction do not cause muscle activity in certain directions to be ignored. In these cases, rather than having a smooth increase in VAF as components are added, there tend to be jumps when the salient features are accounted for. Therefore, we specify a minimum %VAF that should be accounted for in all muscles and all perturbation directions, as well as require that the addition of the next component should not drastically improve the VAFs. Ultimately, however, only an experienced researcher examining the reconstructions of the original raw data traces can determine whether the features accounted for are physiological or are artifacts.

The scree plots from the postural response example demonstrate how five components were selected in this case (Fig. 5.5). Examining the overall VAF (Fig. 5.5A) reveals that one component seems sufficient to explain the variability in the data, using a 75% VAF criterion. However, examining the scree plots for individual
p. 122 muscles reveals that five components are ↳ necessary in order for each of the muscles to achieve ⟩75% VAF (Fig. 5.5B). These curves demonstrate that the activity of GLUT is well accounted for by the first component, but that activity of the other muscles is not. Three components are necessary for VMED to pass the 75% threshold. However, the addition of the second and third components does not change the VAF of TFL and REAB, as illustrated by the flat part of the lines. The fourth and fifth synergies account for the variability in TLF and REAB, respectively. Note that the addition of a sixth component does not drastically improve the VAF in any muscle. Therefore, five muscle synergies were chosen. Examining the variability accounted for across the various perturbation directions leads to a similar conclusion (Fig. 5.5C). Most directions have ⟩ 75% VAF using only one or two components, but there is a sizeable improvement from four to five components for backward perturbations (270 degrees).

Finally, the composition of the components should be examined as additional components are added. The sharp jumps in the scree plots of VAF by muscle and by perturbation direction suggest that including an additional component may cause a previous component to split (Fig. 5.5B, sharp jump in REAB VAF from four to five components). The number of components selected as sufficient to explain the data should be high enough such that the components have stabilized, and the addition of new components does not

significantly change the previous components. In this example, the composition of the components when six components (not shown) were used was compared with the five components identified here and shown not to alter the composition of the five components. Additionally, the reconstructions of the data and the activation coefficients of the sixth component can be used to deduce its contribution to features in the data. If the additional component accounts for a feature, such as a particular burst of muscle activity or tuning direction, that is unaccounted for by the other components, then it may be important; the investigator must decide whether this is a critical and/or physiological feature. If the activation coefficients appear to be evenly distributed across all perturbation directions, it is unlikely to account for a feature associated with muscle activation in a given direction, but is more likely noise.

Using NMF Versus PCA to Test Motor Control Hypotheses: Standing and Walking

Although it is possible to apply either PCA or NMF to any data matrix, the results may not necessarily provide insight into the underlying physiological mechanisms. It is important to ensure that the results are not artifacts of data collection or experimental design. Both techniques allow the dimension of the dataset to be identified. However, the maximum dimension is limited by the number of muscle signals analyzed, as well as by the number of disparate conditions examined. Therefore, it is critical that the ↳ data matrix itself be of high enough dimension such that a reduction in dimension is meaningful. The extraction of components relies on muscles being coordinated in different patterns. Therefore, the number of muscles recorded must be adequately high to capture different patterns of covariation, and the number of experimental conditions or possible variations observed must be of high enough dimension to capture different coordination patterns among the muscles. If muscle activation patterns are truly independent, this will also be reflected in the component analysis.

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For example, the early studies of postural responses examined only two directions of perturbation (forward and backward). It was suggested that there were only two muscles synergies necessary, one active for forward perturbations, and another for backward perturbations (Nashner 1977; Horak and Macpherson 1996). However, these findings revealed experimental rather than physiological constraints. If NMF or PCA were applied only to forward and backward perturbations, they would arrive at a similar conclusion because the data only represent two conditions. By examining multiple perturbation directions, it becomes clear that more than two muscle synergies are needed to describe the full repertoire of postural responses (Macpherson 1988; Macpherson 1991; Henry et al. 1998), but a new muscle synergy is not necessary for each perturbation direction (Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2007). Similarly, the total number of components that can be extracted is limited by the number of muscles that are recorded. It also depends upon muscles being coactivated during certain conditions and not others. Therefore, if only a few muscles are recorded, it is possible that they would each comprise a single synergy if they are independently activated. Conversely, if they are always coactivated, then they will comprise only a single muscle synergy. Again, sufficient experimental conditions must be tested to demonstrate that the muscles could be coactive or independent, depending upon the condition. Such manipulations in pedaling revealed that certain muscles that are always coactive during forward pedaling may have different patterns of activation in backward pedaling (Ting et al. 1999).

Once it is established that the number of muscles and conditions is appropriate and can provide enough variability to extract a smaller number of components, the robustness of such components can then be tested across tasks (Krishnamoorthy et al. 2004; Cheung et al. 2005; d'Avella and Bizzi 2005; Torres-Oviedo et al. 2006). The generality of muscle synergies has been shown in a few studies in which synergies were shared between multiple tasks, such as frog kicking, jumping, and swimming, and in human walking/running, and pedaling forward and backward (Raasch and Zajac 1999; Ting et al. 1999; Cheung et

al. 2005; d'Avella and Bizzi 2005; Cappellini et al. 2006; Torres-Oviedo et al. 2006). Although some synergies are used in multiple tasks, sometimes new synergies emerge when a new motor task is presented
p. 124 (Ivanenko et al. 2005) or the activation of the synergies may be adjusted (Cappellini et al. 2006). ↳

p. 125 Here, we provide two examples of the differences between NMF and PCA when applied to test the robustness of muscle synergies (a) across postural tasks, and (b) during walking.

Are Muscle Synergies Stable or Artifact? Shared Versus Specific Components

Here, we used PCA and NMF to test whether muscle synergies are stable across postural tasks by comparing the components extracted from perturbations in two-legged stance extracted above (Fig. 5.4) to those from perturbations during one-legged stance. Subjects stood on their right leg and were subject to 12 directions of perturbations of smaller velocity and amplitude than in two-legged stance. One- and two-leg data were recorded in the same session, so that the activity of the 16 lower trunk and leg muscles from the stance side could be directly compared.

When PCA was applied to the one-leg data set to identify muscle synergies, two of the components extracted were similar to those identified from the two-leg postural responses (Fig. 5.6A). The first component (W'_{1pca}) is comprised of small contributions from all of the muscles, representing the average responses, so these would be expected to remain the same. Because the similarity between components from one- and two-legged stance are mainly based on the mean level of muscle activity, the VAF provides a better representation of the similarity than r^2 (r^2=0.0291, VAF = 82%). The third component from one-leg
p. 126 responses, W'_{3pca} (Fig. 5.6A, *gray bars*), ↳ looks similar to the second one identified from two-leg responses, W_{2pca} (Fig. 5.6A, *black bars*), suggesting it is more highly activated in two-leg responses. The other components, most of which account for a smaller percentage of variance, are quite different in the one-leg task compared to the two-leg task (max r^2 = 0.176, max VAF=17.5%). Therefore, if PCA were used to identify muscle synergies, the conclusion would be that different muscle synergies are used for one- and two-leg postural responses.

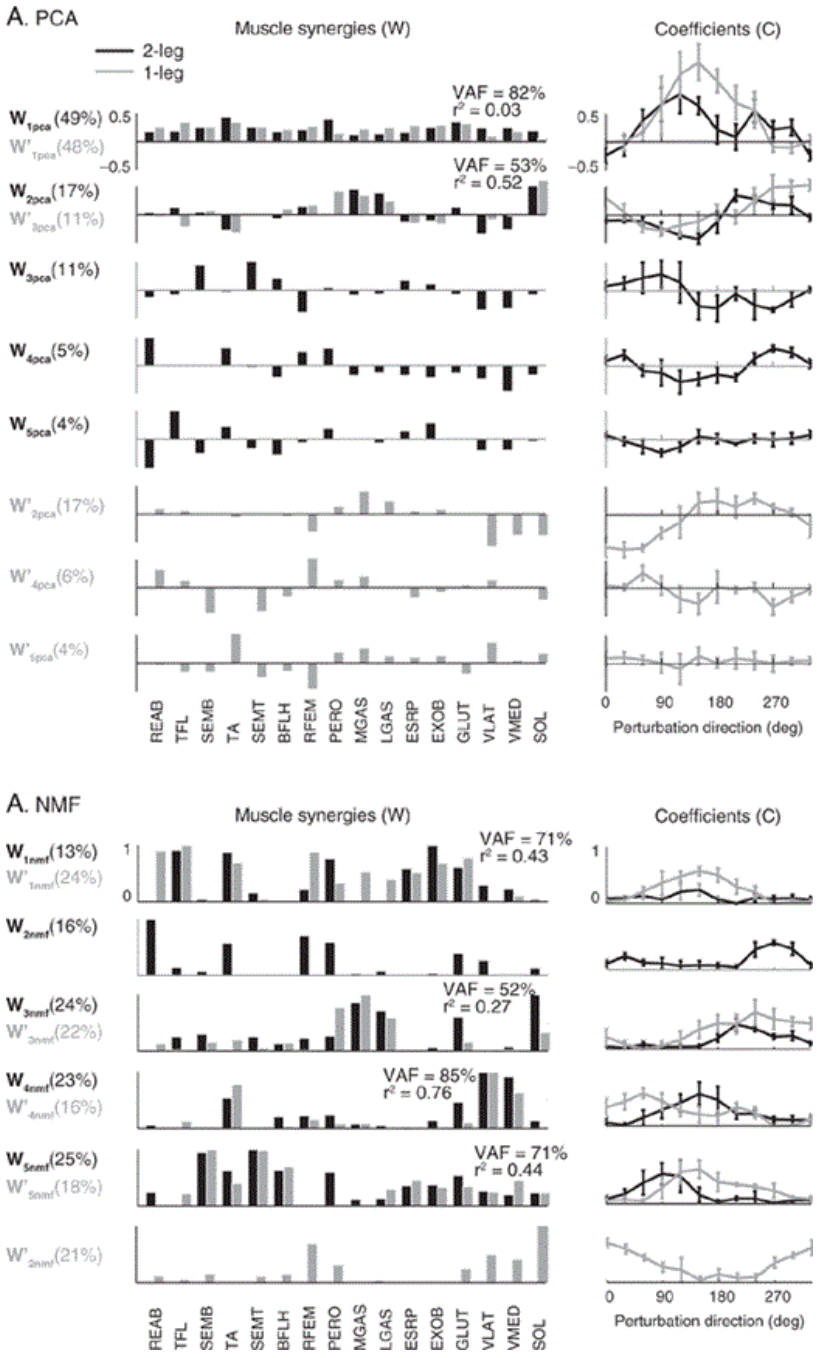

Figure 5.6 Comparison between components identified from one-leg postural responses compared to those identified from two-leg postural responses. **A**: Comparison of components and activation components identified using principal components analysis (PCA). Black bars and lines are two-leg responses (same as in Figure 5.4), and gray bars and lines are one-leg responses. Percentages on the left-hand side of each component represent the percent total variability that each component accounts for. Numbers to the right of each component are indicators of how closely the component from one-leg responses matches the one from two-leg responses. Both r^2 and uncentered r^2 (variability accounted for; VAF) are shown. The first component from one-leg (W'_{1pca}) and two-leg responses (W_{1pca}) matches fairly well, and the third component from one-leg responses (W'_{3pca}) matches the second component from two-leg responses (W_{2pca}). Subsequent components do not match; due to the orthogonality constraint of PCA, when one component changed, subsequent components changed also. **B**: Comparison of components and activation coefficients identified using non-negative matrix factorization (NMF). The same components are used in one-leg and two-leg responses, with the exception of one component that is specific to either condition. The additional component used in one-leg responses is tuned for 0-degree perturbations, which presumably are accounted for by the left leg in two-leg responses. The same components, or muscle synergies, can explain the different individual muscle activations observed between these two tasks, by only changing the activation of the muscle synergies.

When NMF was applied to the one-leg data set to identify muscle synergies, however, four of the five components were very similar to those used during the two-leg balance responses (r^2=0.27 – 0.76, VAF=51%–85%, Fig. 5.6B). The muscle contributions to each of these four components was similar, and the activation coefficient tunings shifted slightly to account for differences in individual muscle tuning curves. The fifth component from two-leg stance (W_{2nmf}) had a large contribution from REAB, a hip flexor, whereas the fifth component in one-leg stance (W'_{5nmf}) has primarily SOL activity, an ankle extensor. This is likely because subjects were more likely to use a hip strategy in two-leg stance compared to one-leg stance. Further, the component used in one-leg stance (W'_{5nmf}) was strongly activated for rightward (0 degree) perturbations. Note that, in the two-leg stance, none of the five components were tuned for rightward perturbation directions (Fig. 5.6B). This suggests that when both legs can be used to respond to a rightward perturbation, subjects use muscles in the left leg to restore their balance, but when the left leg is not available, an additional component in the right leg must be activated to compensate for the loss of stability provided by the left leg. These results show that there are similar components that are used across postural tasks, suggesting that the muscle synergies derived from NMF are physiological constraints that the nervous system uses for muscle coordination, and not simply artifacts of the experiment or analysis.

Although the example demonstrates the possibility of stable components across tasks, thorough cross-validation tests should be performed to ensure that the components are indeed stable across tasks. Therefore, to draw stronger conclusions about the physiological basis of the components, the results of analyses across different subsets and combinations of the data should be compared (e.g., Torres-Oveido and Ting 2010). Apart from extracting components independently from control (e.g., two-leg) and test (e.g., one-leg) tasks, the components from the control condition can be used to reconstruct the test data. If they do not explain a sufficient percentage of the variability, then condition-specific components may be extracted from the remaining variability of the data (Cheung et al. 2005). Additionally, components extracted from the control and test data pooled into one large data set should render similar results. If the same components are identified in all of these cases, it is more likely that the technique has identified underlying physiological features of the data. In our example using NMF, the same components are
p. 127 identified in one-leg and two-leg stance using all ↳ these different combinations (not shown). In contrast, PCA generates different components depending on which data combination is used.

Using Time As a Condition: Muscle Synergies During Walking

When applying PCA and NMF to a continuous motor task, such as locomotion, time can be considered to be a condition. Similar to the different directions of postural perturbations, different coordination patterns
p. 128 across muscles are observed at different timepoints in the locomotor cycle. ↳ However, if muscles are activated in a similar pattern across time, such as in an isometric task, the use of time as a condition may not provide enough variability in the data to allow for meaningful interpretation. In this example, subjects walked freely at a slow (0.7 m/s) pace for at least ten steps each trial. Data were recorded beginning at heel strike of the third to fourth step, so that subjects had already reached a steady-state gait, and each trial includes at least three full stride cycles. Seven trials were included in the data matrix. Sixteen EMG signals were recorded in one leg (Fig. 5.7).

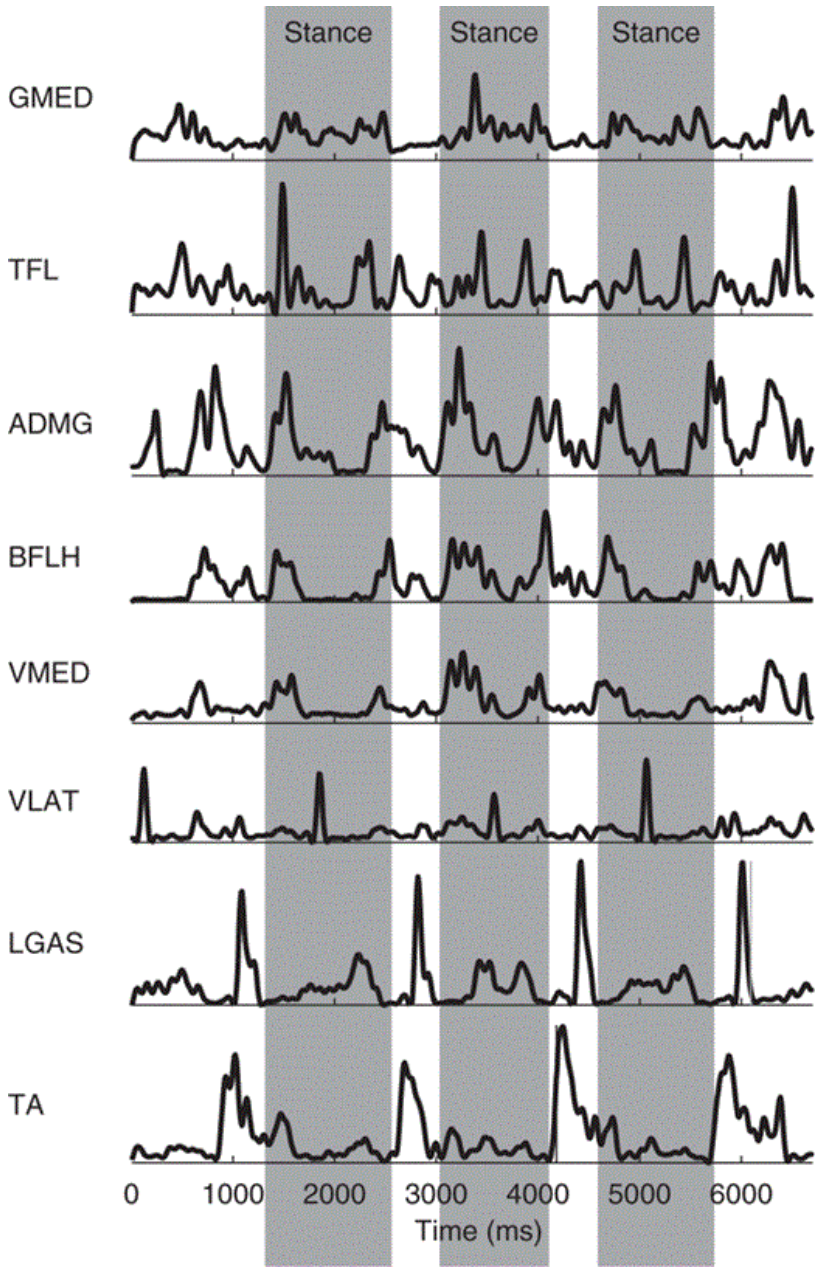

Figure 5.7 Example of muscle activity during a forward walking trial. Shown are eight muscles of the 16 recorded. The subject was walking at a speed of approximately 0.7 m/s. The shaded gray boxes indicate stance phase.

To create the data matrix, the mean activity was computed in 10 ms bins over the three steps in each trial. *Binning* has the advantages of smoothing the data, reducing the total number of conditions, thus reducing computation time, while maintaining much of the detail in the variations of the EMG within and across cycles. Note that the muscle activation patterns do not resemble the idealized sinusoidal EMG patterns often found due to smoothing or averaging. Additionally, the pattern of muscle activity and the duration of the stance phase vary from step to step, as does the number of bins. There is no need to stretch or shorten the data across time to obtain a consistent number of data points per stride. When creating the data matrix, different trials are simply concatenated end to end.

It is important to distinguish between two mutually exclusive hypotheses that can be tested by decomposing
p. 129 walking data into muscle synergies. For both PCA and NMF, the components W_i are assumed to be fixed, ↳

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↳

whereas the activation coefficients or scaling factors c_i are allowed to vary (Clark et al. 2010). Here we choose W's to refer to fixed muscle activation patterns, whereas we allow c's to vary across time. The data must be structured such that the muscles are the observations (rows for NMF, columns for PCA) and the time windows are the conditions (columns for NMF, rows for PCA). Conversely, it is possible to hypothesize that the timing patterns are stereotypical across cycles, and that the muscle coordination patterns vary (Ivanenko et al. 2004; Cappellini et al. 2006). Fixed timing patterns might be generated by a central pattern-generating neural circuit, with their muscle targets changing with phase. In this case, it is necessary to stretch the cycles in time so that they all have the same number of points. In this case, the data should be transposed, such that the time points are the observations, and the muscles are the conditions, with repeated trials or cycles concatenated. However, in neither analysis can both the components and the timing patterns vary. Either muscular coactivation patterns or timing patterns must be assumed to be the same across all conditions.

Here, we compare six components extracted from one subject's walking data using PCA and NMF (Fig. 5.8).

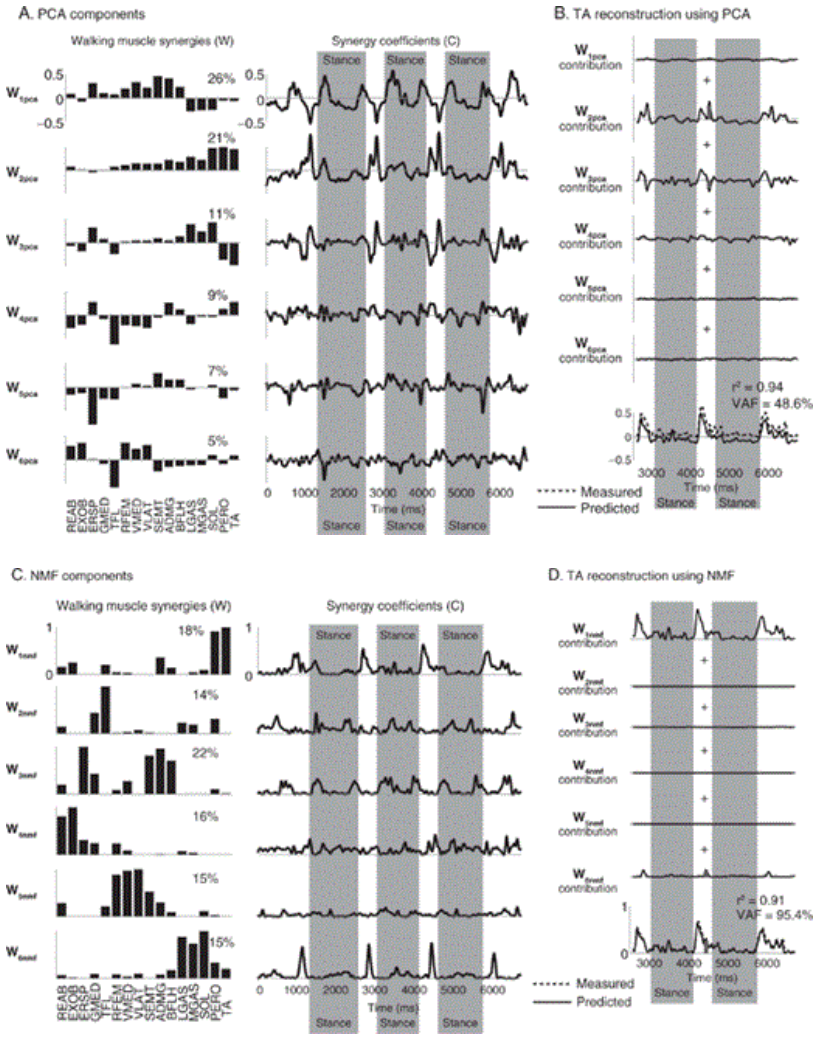

Figure 5.8 Components and activation coefficients identified from walking data using principal components analysis (PCA) and non-negative matrix factorization (NMF). **A**: Components identified using PCA may have positive and/or negative muscle contributions and activation coefficients. Percentages indicate the amount of total data variability accounted for by each component. The shaded gray boxes indicate stance phase. Activation coefficients from one trial of walking (the same trial as in Figure 5.7) are shown. Components from PCA have contributions from many muscles. The first few components have activation patterns that are aligned with particular phases of the gait cycle, whereas the last few have less identifiable patterns. **B**: TA muscle activity from a single trial reconstructed using the PCA components identified in A. The original data are shown with a dashed black line and the reconstructed data are shown with a solid black line. Variability accounted for (VAF) and r^2 indicate goodness-of-fit. **C**: Components identified using NMF have only positive muscle contributions and activation coefficients. Components from NMF tend to have strong contributions from only a few muscles. Activations coefficients for some components (W_{1nmf}, W_{2nmf}, W_{3nmf}, and W_{6nmf}) are aligned with particular phases of the gait cycle, whereas others may be stabilizing components since they are active throughout the entire trial (W_{4nmf} and W_{5nmf}). **D**: TA muscle activity from a single trial reconstructed using the NMF components identified in C. The original data are shown with a dashed black line and the reconstructed data are shown with a solid black line. VAF and r^2 indicate goodness-of-fit.

Similar to the postural response example, the first component identified using PCA primarily describes the mean level of muscle activity, and the later ones described deviations from that mean. The first two components contained primarily positive contributions from nearly all of the muscles. The first component was activated positively at the beginning and end of stance and activated negatively in swing, whereas the second component was positively activated in swing but negatively activated in stance. The subsequent components all had both negative and positive contributions from different muscles, and their activation coefficients over time decreased in amplitude, but increased in frequency. Although the first three

components had peaks that corresponded to identifiable events in the gait cycle and various EMG activity (Fig. 5.7), the last three had high-frequency oscillations that were not localized to a particular phase in the locomotor cycle. Reconstructing the TA EMG signal reveals that the activity during swing phase is composed of contributions from two components primarily, although there are small contributions from all components (Fig. 5.8B). Both components contribute to the large peak in TA activity. However, the smaller, secondary burst is due to a positive contribution from W_{2pca}that is largely cancelled by a negative contribution from W_{3pca}. (Fig. 5.8B). Note that the r^2 value is quite high, indicating a good match of shape, whereas the VAF level is low, indicating that the predicted EMG amplitudes do not match measured values.

The six components extracted using NMF were quite different from those found using PCA. Each component consists of large contributions from a small number of muscles, and the muscles tend to be grouped according to joint or function. Some of the components were activated at specific points during the gait
p. 132 cycle, such as W_{3nmf} being activated at early ↳ stance and again at late stance, W_{1nmf} activated during early swing, and W_{6nmf} during late swing. Other muscle synergies were activated throughout both stance and swing, suggesting that they may be used for stabilization (W_{4nmf} and W_{5nmf}). As in the postural example, the bursts of activity appearing in the activation coefficients resemble the bursts observed in the original EMG data (Fig. 5.7). Only two NMF components contribute to TA EMG activity (Fig. 5.8D). W_{1nmf} contributes most of the TA activity, including the large burst in early swing phase. The contribution from W_{6nmf} adds a small secondary burst.

Again, the components extracted during walking must also be cross-validated over a number of different test extractions to be sure that they are stable and not artifacts of the way the data are represented. In our NMF analyses, we find components to be stable across time bins sizes of 10 to 100 ms during walking. Components are also stable if fewer trials are analyzed, or if faster walking speeds are analyzed. Moreover, the components extracted from one speed can account for variations in EMG occurring with changes in walking speed (Clark et al. 2010). However, the components change if EMGs are averaged across strides, and less of the variability from stride to stride is accounted for by components extracted from averaged data.

Conclusion

Are linear decomposition techniques useful for understanding motor control (Macpherson 1991; Tresch and Jarc 2009)? Ultimately, no decomposition technique is perfect, and much discretion and interpretation must be exercised on the part of the investigator when drawing conclusions from any such analysis. Computational analyses cannot replace the judgment and intuition of the researcher, and ultimately the results must make sense in a physiological context. Therefore, it is critical that the implicit hypotheses, assumptions, and constraints inherent in any technique be understood in order to use it usefully in motor control or other scientific research. In the best-case scenario, a linear decomposition can be a tool that can formally test a hypothesis that the researcher formulates by looking at the raw data and observing the synchrony and variability across multiple EMG signals. It allows different periods of activity within a muscle to be attributed to different underlying components. In the end, the relationship between the derived components and the original data may potentially allow a researcher to draw conclusions about the underlying neural mechanisms if the components do not represent limitations of the recordings, experimental conditions, or other data artifact. Ultimately, to make any sort of physiological conclusion, the extracted components must be interpreted in terms of the known underlying physiological mechanisms and biomechanical outputs. The examples presented here demonstrate intuitively the workings of NMF and
p. 133 PCA, with the aim of informing and aiding in the interpretation ↳ of data. Such exercises can be performed to better understand any kind of decomposition technique, each with its own advantages and disadvantages (Tresch et al. 2006).

Is the added computation useful for understanding motor tasks? In some cases, the answer may be "no," particularly for any kind of initial analysis of a motor task or experimental condition. The technique must appropriately match the hypothesis. Component decompositions can be useful when examining the detailed workings of complex multimuscle coordination. It is useful for comparing complex muscle coordination across different tasks or trials in which muscle activity changes, but the underlying coordination principles may be the same, as we have shown in fast and slow walking (Clark et al. 2010), or one- and two-legged postural control (Torres-Oviedo and Ting 2010). In cases in which repeated measures are not possible, such as in patient populations, highly variable motor patterns are difficult to analyze from traditional techniques that rely on averaging. In this case, a component decomposition can identify whether common underlying elements are being activated across different trials or tasks (Clark et al. 2010). Similarly, the underlying components may provide a better measure of similarity or differences across individuals than the comparison of individual EMG traces (Ting 2007; Ting and McKay 2007). It is possible to identify whether individuals with different EMG patterns have similar underlying components but activate them differently, or if instead they have different numbers or composition of underlying components (Torres-Oviedo and Ting 2007; Clark et al. 2010).

Decomposition can also be useful for understanding the function of the underlying components. These analyses are difficult and do not always work. They require many practical considerations to accommodate limitations of the analysis techniques, and require the investigator to guess at the correct variables that are being controlled. But if a relationship is not found, it does not mean that there is no functional role for that component. Previous work in postural control has shown in cats that muscle synergies are recruited to control forces at the ground (Ting and Macpherson 2005; Torres-Oviedo et al. 2006). Such an analysis includes biomechanical variables as additional observations (rows) in the data matrix and extracts functional muscle synergies, which are composed of both muscles and functional variables (Torres-Oviedo et al. 2006). However, the application of NMF to biomechanical variables poses a challenge because negative and positive changes in forces necessarily result from different muscle groups requiring them to be partitioned physiologically (Ting and Macpherson 2005; Torres-Oviedo et al. 2006; Valero-Cuevas 2009). Because changes in velocity and position require the integration of forces, the relationship between muscle activity and kinematics is highly redundant, and also difficult to predict without explicit models (Gottlieb et al. 1995; Lockhart and Ting 2007). This redundancy is evident in studies relating the activation of components found using PCA to center-of-pressure shifts in human balance control using the uncontrolled manifold hypothesis (Latash et al. 2002; Krishnamoorthy et al. 2003a; Ting and Macpherson 2005). These studies demonstrate that, although functional roles of individual components may be identified, the variability in their activation may not be reflected in the variability of the output because they are precisely coordinated by higher mechanisms in the nervous system to reduce variations in the desired motor task. Alternately, biomechanical simulation and analysis techniques allow the functional role of the muscle coordination patterns identified by the extracted components to be explicitly tested (Raasch et al. 1997; Berniker et al. 2009; Neptune et al. 2009). Additionally, the feasibility of robustly using such components to coordinate a repertoire of movement can also be explored (Raasch and Zajac 1999; Valero-Cuevas 2000; Valero-Cuevas et al. 2003; Kargo and Giszter 2008; McKay and Ting 2008). However, it is difficult to build appropriate dynamics models and to record from all of the muscles involved in a movement to use such techniques. Moreover, models of the neural control mechanisms that shape and use the components effectively need to be explored (Berniker et al. 2009). Again, in order for any of these techniques to be useful in relating muscle activity to functional variables, the investigator must have a good understanding of their raw data and the underlying physiological and biomechanical mechanisms in order to interpret the results of the component analysis appropriately.

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Do the identified components extracted using computational techniques reflect the organization of neural circuits for movement? One of the attractive features of components from NMF is that they generate a parts-based type of representation that appears similar to both neurophysiological observations, as well as

to predictions from "sparse-coding" algorithms in sensory systems (Olshausen and Field 2004). The idea is that in a retinotopic, somatotopic, or other sort of spatial sensory map in the nervous system, only a small region is activated for any given stimulus, such as a location in space, or a part of the body. This "sparse" coding means that a minimum of neurons is used to encode a particular feature from among all of the information contained in that map. But, as in PCA, it is also possible to imagine a system in which neurons in the entire map are activated given a particular stimulus, and their net output results in the identification of a particular stimulus. The sparseness property has also been proposed for motor system, and is proposed to improve energetic expenditure by reducing the number of neurons involved in any given behavior, as well as improving computational efficiency, thus reducing the total number of elements that need to be modified during motor adaptation (Olshausen and Field 2004; Fiete et al. 2007; Ting and McKay 2007). Accordingly, localized regions of motor cortex are activated to perform a given movement, and muscle synergies for reaching have been proposed to result from cortico-motoneuronal cells that project to multiple muscles
p. 135 (Scott and Kalaska 1997; Graziano and Aflalo 2007). Similarly, reticulospinal neurons ↳ active during postural control (Schepens and Drew 2004; Schepens and Drew 2006; Schepens et al. 2008; Stapley and Drew 2009) also project to multiple muscles in the limbs and trunk, and interneurons in the spinal cord may facilitate coordination of muscles within and between the limbs during locomotion (Quevedo et al. 2000; McCrea 2001; Drew et al. 2008).

Although, NMF components may provide one computational tool among the many needed to understand the sensorimotor transformations involved in determining how we move, much research is warranted before any of the questions about the utility and interpretability of the resulting components can be resolved. Component decompositions allow large datasets of EMG data and other variables to be decomposed into components that must be interpreted and compared to the organization of neural control systems upstream, and their functional biomechanical outputs downstream. NMF is especially useful for examining neural and muscle activity signals that are inherently non-negative. PCA may prove more useful for analyzing biomechanical variables that take on both positive and negative values without consideration for muscle activity. The continued development of physiologically relevant decomposition techniques combined with experimental and computational studies may eventually allow us to better understand how learning, adaptation, and rehabilitation occurs in the motor system.

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