

A Limited Set of Muscle Synergies for Force Control During a Postural Task

Lena H. Ting and Jane M. Macpherson

Neurological Sciences Institute, Oregon Health and Sciences University, Beaverton, Oregon; and Department of Biomedical Engineering, Emory University and Georgia Institute of Technology, Atlanta, Georgia

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Ting, Lena H. and Jane M. Macpherson. A limited set of muscle synergies for force control during a postural task. *J Neurophysiol* 93: 609–613, 2005. First published September 1, 2004; doi:10.1152/jn.00681.2004. Recently developed computational techniques have been used to reduce muscle activation patterns of high complexity to a simple synergy organization and to bring new insights to the long-standing degrees of freedom problem in motor control. We used a nonnegative factorization approach to identify muscle synergies during postural responses in the cat and to examine the functional significance of such synergies for natural behaviors. We hypothesized that the simplification of neural control afforded by muscle synergies must be matched by a similar reduction in degrees of freedom at the biomechanical level. Electromyographic data were recorded from 8–15 hindlimb muscles of cats exposed to 16 directions of support surface translation. Results showed that as few as four synergies could account for >95% of the automatic postural response across all muscles and all directions. Each synergy was activated for a specific set of perturbation directions, and moreover, each was correlated with a unique vector of endpoint force under the limb. We suggest that, within the context of active balance control, postural synergies reflect a neural command signal that specifies endpoint force of a limb.

INTRODUCTION

Active balancing requires controlling a large number of muscles and joints across all four limbs, trunk, and neck. The concept of synergies was proposed by Bernstein (1967) as a strategy for grouping output variables to simplify control. Previous attempts to identify muscle synergies failed to account for the high degree of complexity in natural behaviors because they assumed that each muscle may belong to only one synergy (Buchanan et al. 1986; Lee 1984; Macpherson 1991; Soechting and Lacquaniti 1989). Thus the use of synergies for analyzing natural motor behaviors was questioned (Macpherson 1991). Recently, synergies at the muscle activation level have been identified using nonnegative matrix factorization (Tresch et al. 2002). With this technique, each muscle can be simultaneously activated by multiple synergies, so no two muscle activation patterns are exactly alike, yet significant partial correlations may exist across many muscles. These findings suggest that the nervous system may use a limited set of control signals to activate a large number of muscles, yet still achieve the flexibility and variability characteristic of natural behaviors.

If synergies exist, what is the nature of the command signal, and furthermore, what is the biomechanical significance of each synergy? We hypothesized that the modularity in control afforded by a synergy organization must be matched by a similar reduction in degrees of freedom at the biomechanical

level. To this end, we studied how synergy activation levels and biomechanical signals varied during the automatic postural response in cats to linear translation of the support surface in 16 directions in the horizontal plane.

Feline postural responses have been well characterized and are sufficiently complex for investigating how synergies can control natural behaviors. For each direction of translation, a different pattern of EMG activity and active force is elicited to stabilize balance (Macpherson 1988a,b). The purpose of this report is to examine the synergy organization of this natural behavior and to test whether the synergies were related to the functional, biomechanical variable of endpoint force between the limb and the support surface.

METHODS

EMG activity was recorded in three cats from 8, 11, and 15 left hindlimb muscles (for details, see Macpherson 1988b). The freely standing cats were exposed to ramp-and-hold translations of the support surface of 5-cm amplitude and 15-cm/s mean maximum velocity. Five trials were collected for each of 16 perturbation directions evenly spaced in the horizontal plane (Fig. 1C, *inset*) across 3 days. Ground reaction forces and raw EMGs were collected at 1,000 Hz and processed off-line using MATLAB (Mathworks): force data were low-pass filtered at 100 Hz, and EMG data were high-pass filtered at 35 Hz, demeaned, rectified, and low-pass filtered at 35 Hz. Data were averaged across like trials. Mean EMG activity was computed for the automatic postural response during the time window of 60–135 ms after platform movement onset and normalized within each muscle to the maximum response across all perturbation directions. The mean active force response was computed for the period of 120–195 ms after perturbation onset (cf. Jacobs and Macpherson 1996). EMG responses were plotted as a function of perturbation direction, termed EMG tuning curves.

Synergy analysis

EMG responses were analyzed using a nonnegative optimization procedure similar to that described by Tresch et al. (1999). It was assumed that 1) any given muscle can belong to more than one synergy and 2) the muscles within a given synergy have a fixed proportional activation. For example, given three muscles, each synergy, \mathbf{W}_i , is represented as a 3×1 vector (with constant elements w_{i1} , w_{i2} , w_{i3}) that specifies the relative activation level of each muscle between 0 and 1 (Fig. 1A, red and blue boxes). When a synergy is recruited during a motor task, each element in the synergy vector \mathbf{W}_i is multiplied by a scaling coefficient, c_i , yielding a specific pattern of muscle activity $c_i \cdot \mathbf{W}_i$ (Fig. 1A, red or blue lines). Because several synergies may act on a given muscle, the net activation of that muscle is the sum of activations due to each synergy. In Fig. 1A, the total activity of muscle 1 is $c_1 \cdot w_{11} + c_2 \cdot w_{21}$. In general, the ensemble

Address for reprint requests and other correspondence: L. H. Ting, Wallace H. Coulter Dept. of Biomedical Engineering at Georgia Tech and Emory Univ., 313 Ferst Dr., Atlanta, GA 30322-0535 (E-mail: lting@emory.edu).

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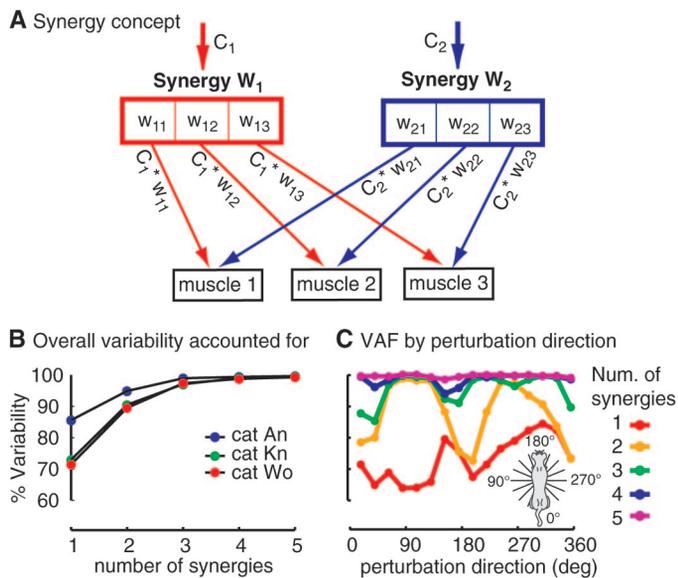


FIG. 1. A: muscle synergy concept and mathematical implementation. B: percent of overall variability accounted for (VAF) in the EMG signals as a function of number of synergies chosen. C: percent of VAF accounted for as a function of perturbation direction for 1–5 synergies. Although 2 synergies account for >90% total VAF, when each perturbation direction is considered individually, responses in many directions are poorly reconstructed (orange line). With >4 synergies, improvements affect all directions roughly equally.

EMG pattern can be expressed as the weighted sum of synergies, $EMG = \sum_{i=1}^{N_{syn}} W_i \cdot c_i$. The pattern of each synergy's activation level over the 16 perturbation directions is expressed as a 16×1 vector C_i (with elements $c_{i1}, c_{i2}, \dots, c_{i16}$). C_i represents the command to synergy W_i and expresses how the synergy activation varies as a function of direction (synergy tuning curves).

In the optimization procedure, the number of synergies is first specified by the user, and the elements of each synergy vector are randomly assigned initial values. A gradient search algorithm (MATLAB function `fmincon.m`) varies the elements of each synergy, w_{i1}, w_{i2}, \dots , to minimize the difference between the actual data and the reconstructed muscle activation pattern, using additive linear combinations of the synergies. At each iteration, the reconstruction coefficients c_{ij} are found using a nonnegative least squares fit (MATLAB `lsnonneg.m`) of the synergies to the data. This process is continued until the least-squared errors between EMG data and the reconstructed EMG values are minimized. The same synergy vectors were found over repeated optimizations with random initial conditions.

Optimizations for each cat were run using one to six synergies. The number of synergies that best characterized the data were determined using two criteria: 1) that a large percentage (>95%) of the total variability was accounted for (VAF) over the entire run and 2) that the distribution of errors as a function of perturbation direction was roughly uniform. These two criteria ensured that each synergy chosen added a component that was necessary so that muscle activation patterns in each perturbation direction were adequately reconstructed. Whereas the addition of a synergy might increase the global VAF by only a few percentage points, synergy was included if it improved the reconstruction of specific muscle activation patterns in response to particular perturbation directions. If adding a synergy improved the reconstruction only incrementally and roughly equally across all directions, the synergy probably accounted for random variations and was not added. At least five optimizations were performed for each set of synergies, and the VAF varied by <0.01% across all optimizations with the same number of synergies.

Decomposition of ground reaction forces

To test the hypothesis that activation of each muscle synergy generates a unique direction of endpoint force, we decomposed the change in applied force at the left hindpaw into basis force vectors using the same nonnegative factorization technique describe above. The basis force vectors are analogous to muscle synergies: a set of nonorthogonal basis force vectors that are scaled by activation coefficients are extracted. Thus the nonnegative routine removes any dependence on the defined Cartesian coordinate system and essentially determines a new, nonorthogonal, force coordinate system that can reconstruct the entire force response data for all directions of translation. This analysis also allowed us to determine the number of degrees of freedom in the biomechanical output variable of force applied by the hindlimb to the ground. First, the change in active force response was computed for each x , y , and z component, by subtracting the mean background levels prior to the perturbation. Force changes of opposite sign elicit responses in different muscles; for example, loading of the limb ($+F_z$) elicits an active extensor response, whereas unloading ($-F_z$) elicits an active flexor response (Macpherson 1988a,b). Thus the positive and negative changes in force were separated, resulting in six different vectors representing the positive and negative changes in F_x , F_y , and F_z applied forces. If the change in force was positive for a given direction, the corresponding negative component was set to zero. Each force direction was normalized to its own maximum value to eliminate the magnitude differences between vertical and horizontal force changes. The absolute value of these six values for each of the 16 directions of translation were input to the nonnegative factorization. As in the EMG analysis, the number of basis force vectors was determined by optimizing how well a set of nonorthogonal basis force vectors could reconstruct the changes in applied force over all perturbation directions. These basis force vectors were converted back to force units, and the activation levels of muscle synergies were correlated to the activation levels of the basis force vectors across perturbation direction.

RESULTS

Four muscle synergies and four basis force vectors were sufficient to reproduce the complex postural response data set for all three cats. Furthermore, the activation pattern of each synergy was correlated with the modulation of a specific basis force vector, suggesting that postural synergies may be organized to control endpoint force during balance tasks.

Number of synergies

Using both global and local criteria, four synergies were found to reliably reproduce >95% variability in EMG patterns across all perturbation directions (Fig. 1B) and to reproduce >90% variability in any single perturbation direction (Fig. 1C). Although the addition of a fifth or higher synergy increased the overall VAF, the improvement was incremental and evenly spread across all perturbation directions. In contrast, with three synergies, the VAF for some directions dropped <90% even though overall VAF exceeded that value in all cats.

Muscle synergy composition

Each synergy was characterized by a dominant subset of muscles with relatively high weights and the remainder with low or zero weights (Fig. 2A). Most muscles were activated by more than one synergy, but usually predominated in only one synergy and exhibited lower weights in the others. Moreover,

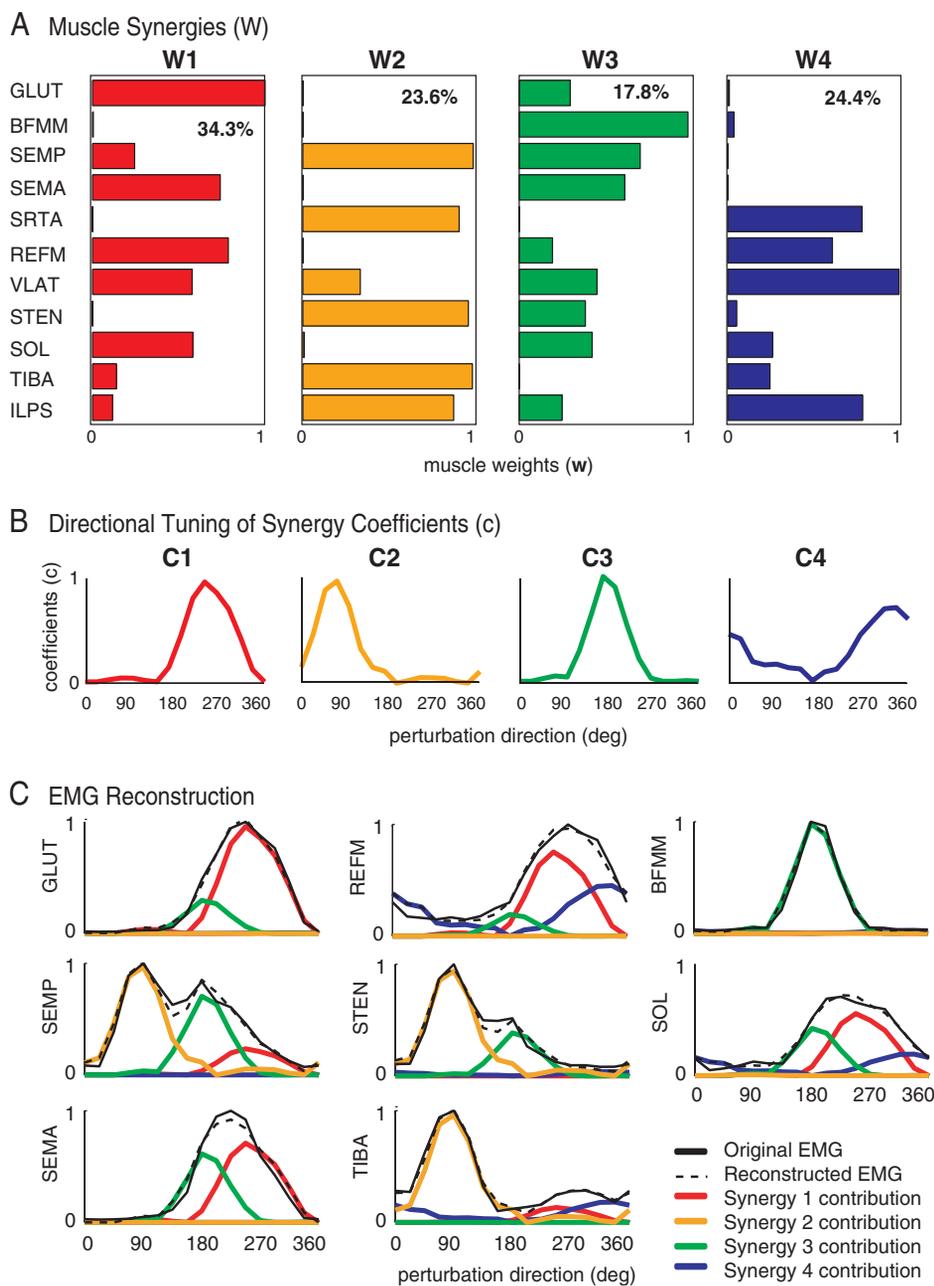


FIG. 2. *A*: muscle synergy composition for the case where 4 synergies are chosen. Note that each muscle may be activated to a different degree by each muscle synergy. Percentages shown represent the percent total VAF accounted for by activation of each synergy. GLUT, gluteus medius; BFMM, biceps femoris middle head; SEMP, posterior semimembranosus; SEMA, anterior semimembranosus; SRTA, anterior sartorius; REFM, rectus femoris; VLAT, vastus lateralis; STEN, semitendinosus; SOL, soleus; TIBA, tibialis anterior; ILPS, iliopsoas. Data taken from cat Kn. *B*: synergy activation coefficients, C_i . These tuning curves represent the degrees to which each synergy is active during each perturbation direction. *C*: EMG tuning curves reconstructed using synergies. Each muscle's tuning curve is found by summing the product of each tuning curve, C_i , and the weighting of each muscle within the synergy W_i . All muscle tuning curves are thus constrained to be weighted averages of synergy tuning curves. Therefore muscle tuning curves have more varied and complex shapes than synergy tuning curves. Dashed lines, experimental data; black solid lines, reconstructed data; colored lines, contributions from each synergy.

each synergy was comprised of muscles crossing all of the hindlimb joints including both uni- and biarticular muscles. For example in cat Kn, gluteus medius (GLUT) was activated by synergies W_1 and W_3 (Fig. 2A), middle biceps femoris (BFMM) was primarily activated by W_3 , and posterior semimembranosus (SEMP) was activated by synergies W_1 , W_2 , and W_3 . Furthermore, W_1 was dominated by extensors of the hip, knee, and ankle and W_2 by flexors, whereas W_3 and W_4 tended toward higher activations in biarticular thigh muscles. Six of the recorded muscles were common across all three cats, allowing us to compare the synergy composition across subjects. The weightings (w_i) for those six muscles were correlated across cats for each of the four synergies. Coefficients of determination (r^2) between cat An and cats Kn and Wo, respectively, for the first synergy (W_1) were 0.96 and 0.89. For W_2 , they were 0.71 and 0.72, for W_3 , they were 0.90 and 0.80,

and for W_4 , they were 0.52 and 0.66. Thus synergy composition is robust across subjects and reflects the consistency in the EMG tuning curves of the postural response (Macpherson 1988b).

Muscle synergy tuning curves

The activation level of each muscle synergy (coefficients C_i) varied with perturbation direction with a single, monophasic peak at a characteristic direction. (Fig. 2B). This “synergy tuning curve” may be considered as the neural command signal to the synergy, which activates a pattern of muscles appropriate to the postural response. For each perturbation direction, a unique pattern of synergies is activated. For example, for a rightward perturbation at 270°, W_1 and W_4 are activated, but W_2 and W_3 are not. The directions and shapes of the synergy

tuning curves were quite similar across cats. Peak activation for W_1 occurred at 202, 180, and 225° for cats An, Kn, and Wo, respectively. Peak activation for W_2 occurred at 247, 270, and 337°; peak activation for W_3 occurred at 90, 90, and 135°.

Reconstruction of EMG tuning curves

Because the EMG data were reconstructed as a weighted sum of synergies at each perturbation direction (Fig. 2C), the tuning curves of each muscle could only take the shape of additive linear combinations of the synergy tuning curves, C_i . For example, the tuning curve of GLUT results from the synergy tuning curve C_1 multiplied by the value of the GLUT weighting in W_1 (Fig. 2, A and B; red), plus the synergy tuning curve C_3 multiplied by the value of the GLUT weighting in W_3 (Fig. 2, A and B; green). BFMM is activated by W_3 only, and therefore, has the same single peak as C_3 , whereas SEMP has two peaks due to activation by both W_2 and W_3 . Thus EMG tuning curves were partitioned according to each synergy's contribution to the activity. The reconstructed EMG tuning curves closely matched the original data (compare solid black lines and dashed black lines in Fig. 2C).

Relationship between muscle synergies and hindlimb force

The synergy activation tuning curves, C_i , were significantly correlated with the activation of individual basis force vectors (Fig. 3), suggesting a functional association between muscle synergies and limb endpoint force. The change in force applied by the limb to the ground following perturbations (Fig. 3A) was decomposed into four nonorthogonal basis force vectors that

each pointed in a different direction (Fig. 3B). The magnitude of each basis force vector varied as a function of perturbation direction similar to the synergy tuning curves, and each matched-pair of synergy and force tuning curves were significantly correlated (Fig. 3C). The extensor synergy (W_1) was associated with a downward and outward force, the flexor synergy (W_2) with an upward and inward force, and synergy W_3 primarily with a lateral force. Synergy W_4 showed the lowest correlation with endpoint force vector.

DISCUSSION

These results show that a natural behavior of high complexity (multiple muscles and directions of perturbation) can be reduced to coordinative patterns of low dimensionality that correspond to task-level biomechanical functions for balance. We propose that the nervous system may use such a simplifying control structure for coordinating movement in general. Each muscle synergy would be activated as a function of the desired biomechanical outcome, thereby simplifying the transformation from task-level variables to muscle activation patterns. Thus the number of degrees of freedom in the biomechanical output would be limited by the number of muscle synergies used by the nervous system.

The automatic postural response is highly stereotyped and repeatable (Macpherson 1988a,b), and these features are reflected in the robustness of the synergy composition and tuning across days and across cats. We chose to examine the relation of synergies to endpoint force because maintaining balance is inherently a force control task—forces applied against the support surface act to accelerate the center of mass. Moreover, our recent study suggested that paw afferents encoding change in endpoint force at the support surface provide the sensory cues for selection of the appropriate muscle pattern, or synergy activation, in the postural response (Ting and Macpherson 2004). The first two synergies, W_1 and W_2 were dominated by the antigravity-related functions of loading and unloading of the limb. It is likely that the third synergy fine-tuned the horizontal plane forces, contributing to the previously reported force constraint strategy in the response to translation, in which the applied forces tend to group around two main directions in the horizontal plane, regardless of the direction of translation (Macpherson 1988a). The fourth synergy, W_4 , had the lowest correlation to active force production at the ground, with a peak activation at 337°. In this direction, the left hindlimb generated very little change in force, while the contralateral, right hindlimb played a large role in stabilizing the body by applying an unloading force directed forward and medially. Thus, rather than generating a specific endpoint force, W_4 may have acted to stiffen the leg, perhaps to minimize unwanted effects from the strong flexor activation of the contralateral leg and to stabilize the pelvis. Furthermore, the mechanical interactions between the limbs could also account for the portions of the ground reaction forces that are not matched to synergy activations.

The correspondence between synergies and whole limb force is consistent not only with balance control but also with pedaling for which muscle groupings correlate with accelerations of the toe relative to the hip (Ting et al. 1999) and vary in amplitude as a function of the sensorimotor state of the task (Ting et al. 2000). We expect that other variables—kinematic, kinetic, and impedance—may also be controlled by a muscle

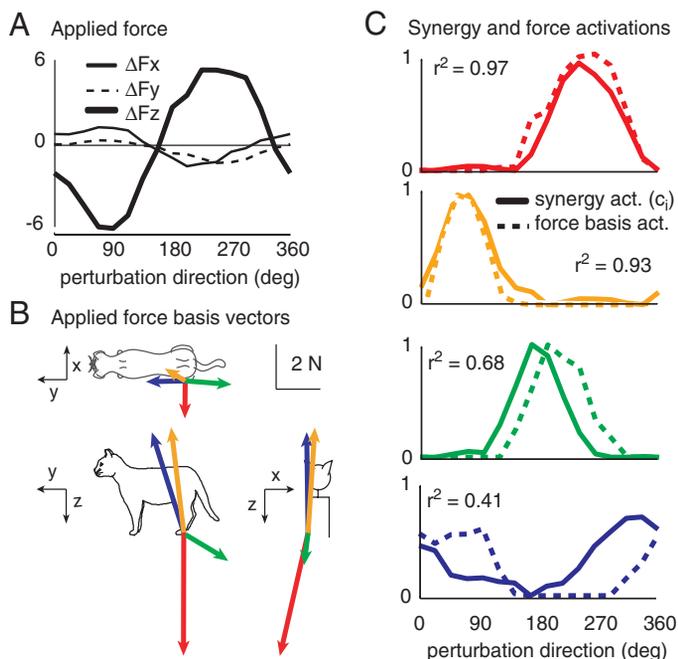


FIG. 3. A: active changes in force at the ground applied by the left hindlimb during the postural response. B: each colored line represents 1 of the 4 basis force vectors that are sufficient for reproducing active changes in applied forces. C: tuning curves representing the activations of basis force vectors as a function of perturbation direction (dotted lines) are highly correlated with synergy tuning curves, C_i (solid lines), suggesting that the synergies each produce a force in the direction of the corresponding basis force vector. r^2 , correlation coefficient.

synergy organization, depending on the task (Ivanenko et al. 2003; Krishnamoorthy et al. 2003a,b). By including these variables, the number of possible degrees of freedom in biomechanical outputs is vastly increased. For example, Saltiel et al. (2001) showed that similar kinematics, such as leg extension, could be produced by synergies with different muscle activations, although the movements might be different under different loading conditions. We anticipate that there are many synergies involved in the performance of different types of tasks.

Advantages of our technique include the extraction of physiologically interpretable components and the fact that synergy organization can be identified without a priori knowledge of function (cf. Jacobs and Macpherson 1996; Raasch and Zajac 1999). Nonnegative methods are more successful than strictly orthogonal methods like principal components analysis (PCA) at breaking complex objects into meaningful parts, particularly in such inherently positive-valued data as neural spike trains or muscle activations (Lee and Seung 1999). Basis vectors only add and never subtract features, and they are nonorthogonal. Therefore each synergy's activation can be analyzed independently, whereas in PCA, many features of the components cancel each other out on data reconstruction, which means that their contribution to the final output pattern depends on the activity of other synergies. In contrast, the extracted components in nonnegative techniques are based on the compositionality of the data set, rather than holistic features. For example, when applied to images of faces, a nonnegative extraction routine generates basis vectors representing noses, ears, and eyes, whereas PCA generates components that all tend to look roughly like an entire face (Lee and Seung 1999). A limitation of our technique is that proper identification of muscle synergies requires a high degree of complexity in the sampling of muscle coordination patterns. If, for example, only two perturbation directions had been studied, only two muscle synergies would have been identified. For our paradigm, similar synergies could be extracted from as few as 8 of the 16 perturbations directions.

Our approach may be useful for understanding neural feedback control and biomechanical functions of muscle synergies in natural behaviors. The idea that muscle synergies produce whole limb functions is consistent with the findings that sensory signals arising from the spinal cord can represent integrative variables such as limb length and limb orientation (Bosco et al. 2000). It is also consistent with recent studies suggesting that focal stimulation of the spinal cord may produce consistent patterns of muscle activation (Ivanenko et al. 2003; Lemay and Grill 2004; Saltiel et al. 2001; Tresch et al. 2002). Thus muscle synergy activations could be modulated directly by such sensory signals to control overall limb function, allowing higher CNS levels to encode task-level variables without regard for individual muscle activations. Our synergy analysis may provide a pattern that varies more closely with neural signals than biomechanics or individual muscle activation patterns. It remains to be seen whether the synergy organization can be used to control a wide range of activities, and the extent to which synergies are shared across different types of tasks.

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