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Common muscle synergies for control of center of mass and force in nonstepping and stepping postural behaviors

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Chvatal SA, Torres-Oviedo G, Safavynia SA, Ting LH. Common muscle synergies for control of center of mass and force in nonstepping and stepping postural behaviors. *J Neurophysiol* 106: 999–1015, 2011. First published June 8, 2011; doi:10.1152/jn.00549.2010.—We investigated muscle activity, ground reaction forces, and center of mass (CoM) acceleration in two different postural behaviors for standing balance control in humans to determine whether common neural mechanisms are used in different postural tasks. We compared nonstepping responses, where the base of support is stationary and balance is recovered by returning CoM back to its initial position, with stepping responses, where the base of support is enlarged and balance is recovered by pushing the CoM away from the initial position. In response to perturbations of the same direction, these two postural behaviors resulted in different muscle activity and ground reaction forces. We hypothesized that a common pool of muscle synergies producing consistent task-level biomechanical functions is used to generate different postural behaviors. Two sets of support-surface translations in 12 horizontal-plane directions were presented, first to evoke stepping responses and then to evoke nonstepping responses. Electromyographs in 16 lower back and leg muscles of the stance leg were measured. Initially (~100-ms latency), electromyographs, CoM acceleration, and forces were similar in nonstepping and stepping responses, but these diverged in later time periods (~200 ms), when stepping occurred. We identified muscle synergies using non-negative matrix factorization and functional muscle synergies that quantified correlations between muscle synergy recruitment levels and biomechanical outputs. Functional muscle synergies that produce forces to restore CoM position in nonstepping responses were also used to displace the CoM during stepping responses. These results suggest that muscle synergies represent common neural mechanisms for CoM movement control under different dynamic conditions: stepping and nonstepping postural responses.

balance; electromyograph; falls; human; posture

MUSCLE SYNERGIES have been proposed to be a modular organization for muscle coordination that map high-level task goals, or motor intentions, into motor actions (Chiel et al. 2009; Drew et al. 2008; Giszter et al. 2007; Ting and McKay 2007; Yakovenko et al. 2010). Here, we explicitly tested this hypothesis by investigating the relationship between muscle synergy recruitment and functional motor outputs in two postural tasks, stepping and nonstepping responses to perturbations, that achieve the same motor intention of maintaining upright balance using different motor actions. Muscle synergies and other types of modular organization have been used to explain muscle coordination during a variety of motor behaviors in many different species (Cappellini et al. 2006; d'Avella et al. 2006; d'Avella et al. 2003; Drew et al. 2008; Flash and Hochner 2005; Hart and Giszter 2004; Kargo and Giszter 2000; Krishnamoorthy et al. 2004; Latash et al. 2005; Ting and Macpherson 2005; Torres-Oviedo et al. 2006; Yakovenko et al. 2010). The generality of muscle synergies across different motor tasks has been shown in frog kicking, jumping, and swimming (Cheung et al. 2005; d'Avella and Bizzi 2005) or in human walking and running (Cappellini et al. 2006) or in forward and backward pedaling (Raasch and Zajac 1999; Ting et al. 1999). Although some muscle synergies are used across multiple tasks, in some instances, new synergies may emerge when a new motor task is presented (Cheung et al. 2005; Ivanenko et al. 2005; Robert et al. 2008; Torres-Oviedo and Ting 2010), and the recruitment of the synergies may be altered (Cappellini et al. 2006; Clark et al. 2010).

The recruitment of these muscle synergies, or motor modules, may be related to specific biomechanical functions necessary to accomplish a behavioral goal (Berniker et al. 2009; Chiel et al. 2009; Giszter et al. 2007; Raasch and Zajac 1999; Ting and McKay 2007). Muscle synergies in humans have been correlated with foot kinematics in locomotion (Ivanenko et al. 2003; Ivanenko et al. 2006) and foot acceleration in pedaling (Ting et al. 1999). The biomechanical outputs related to muscle synergies depend on the motor task being performed. In human finger spelling, muscle synergies are correlated with common hand postures (Weiss and Flanders 2004), whereas in frog kicking, jumping, and swimming, shared muscle synergies may be activated to implement whole limb movements common to these locomotor behaviors (Cheung et al. 2005; d'Avella and Bizzi 2005). In balance control, we found that muscle synergies in the cat are recruited to produce specific force vectors at the ground that are robust across changes in postural configuration (Ting and Macpherson 2005; Torres-Oviedo et al. 2006). Although these correlations indicate possible muscle synergy functions, the stimuli triggering the studied movements and the behavioral outputs were also directly related. Therefore, one purpose of this study was to determine whether muscle synergies map high-level task goals into actions independently from sensory inputs triggering the postural response.

In feline standing balance control, it has been hypothesized that several muscle synergies are recruited to control center of mass (CoM) kinematics by modulating end-point forces (McKay and Ting 2008; Torres-Oviedo et al. 2006), but similar studies have not been conducted in human balance control. Our previous work in human balance control has shown that the same muscle synergies can account for balance responses across a variety of standing conditions (Torres-Oviedo and Ting 2010), suggesting that these motor modules may produce biomechanical functions generally needed for balance control.

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It is likely that these biomechanical functions are related to the control of CoM motion. Human balance control is complex as a broad range of postural behaviors is available in response to perturbations, such as the so-called hip and ankle strategies (Horak and Macpherson 1996; Runge et al. 1998), stepping (McIlroy and Maki 1993b), or using the upper extremities for stabilization (Maki and McIlroy 1997). In any variation of the standing balance task, maintaining balance requires keeping the CoM above the base of support (BoS) (Massion 1992; Scholz et al. 2007; Ting et al. 2009). During feet-in-place postural response behaviors, however, the muscles recruited for postural stabilization depend on the direction of CoM motion, rather than the local changes in joint angle displacements (Carpenter et al. 1999; Gollhofer et al. 1989; Ting and Macpherson 2004). Similarly, CoM kinematics can predict the activation time course of distal and proximal muscles (Welch and Ting 2008), suggesting a neural command reflecting CoM kinematics could activate multiple muscles across the body.

Here, we used support-surface perturbations to elicit both stepping and nonstepping postural responses, allowing us to test the hypothesis that muscle synergies are recruited to achieve the biomechanical output of controlling CoM, independent of the sensory input triggering the response. In nonstepping postural responses to perturbations, the feet stay in place and the CoM is returned back to its initial position above the feet. Conversely, in stepping responses, the BoS is expanded by taking a step, which results in the CoM being displaced even further from the initial position. Therefore, in these two behaviors, the motor output, or desired direction of CoM movement, is opposite in response to the same direction of perturbation, which evokes similar sensory inputs in the two cases. Comparing these two postural behaviors allows dissociation among patterns of somatosensory input (due to perturbation direction), the associated patterns of muscular output, and the resultant CoM motion.

To use muscle synergy analysis to examine stepping responses, it was first necessary to characterize muscle activity in multidirectional stepping responses more thoroughly. Very few studies have examined the patterns of electromyographs (EMGs) during stepping responses and compared these patterns to those observed in nonstepping responses (Horak and Macpherson 1996; McIlroy and Maki 1993a). The magnitude of the initial EMG is increased in stepping responses compared with nonstepping responses (McIlroy and Maki 1993a), but the time course of muscle activity during stepping and nonstepping responses has not been compared. Furthermore, stepping responses in directions other than anterior/posterior and medial/lateral directions have not been examined. Multidirectional tuning curves are necessary to fully evaluate patterns of underlying muscle synergies. Therefore, in this study, we compared the initial time course of muscle activity in stepping and nonstepping responses and characterized muscle activity tuning during stepping responses to multidirectional perturbations other than previously investigated anterior/posterior and medial/lateral (Perry et al. 2000; Zettel et al. 2002).

We hypothesized that by differentially recruiting a common pool of muscle synergies with specific biomechanical functions, the central nervous system can direct the movement of the CoM in both nonstepping and stepping postural responses. We first determined whether the same muscle synergies were recruited in both stepping and nonstepping postural responses to perturbation or whether different sets of muscle synergies were recruited during these two postural strategies. Furthermore, we examined whether the recruitment of muscle synergies in both types of response was related to a consistent biomechanical function such as to displace the CoM or to produce particular forces in a particular direction or whether the recruitment was related to perturbation direction. We predicted that the same muscle synergies would be used in the stance leg during both stepping and nonstepping postural behaviors to produce similar forces at the ground and CoM acceleration in the two behaviors but that the recruitment of these functional muscle synergies would differ across stepping and nonstepping responses depending on the desired direction of CoM motion. Alternatively, if muscle synergies were instead patterned in direct response to somatosensory feedback, we would expect to see the same muscle synergies activated for the same perturbation directions in both nonstepping and stepping responses, even when the resulting CoM acceleration was in opposite directions.

METHODS

To determine whether the same muscle synergies are recruited during nonstepping and stepping postural behaviors, and whether they are related to a behavioral goal, we recorded human postural responses to support surface translations. Twelve ramp and hold perturbation directions were applied in the horizontal plane, and the presentation order was randomized. Subjects were instructed to maintain their balance and to step with their left foot if a step was necessary to recover their balance. Subjects participated in two sets of perturbations: the first was a larger, faster set that caused a stepping response and the second was a smaller, slower set, during which they maintained balance without moving their feet. Muscle synergies were extracted from the nonstepping condition and the stepping condition individually and compared; muscle synergies extracted from nonstepping trials were subsequently used to reconstruct the stepping trials. If the stepping data were not sufficiently explained by the nonstepping muscle synergies, additional stepping-specific muscle synergies were then extracted. Finally, we identified functional muscle synergies by incorporating kinematic and kinetic data into our data set for analysis to determine whether the recruitment of muscle synergies was correlated to the production of a consistent biomechanical function.

Data collection. Eight healthy subjects (5 men and 3 women) between the ages of 21 and 27 yr were exposed to two sets of support-surface translations according to an experimental protocol that had been approved by the Institutional Review Boards of Georgia Tech and Emory University. Subjects stood on a platform that translated in 12 equally spaced directions in the horizontal plane (see Fig. 1). They were instructed to maintain balance without stepping if possible, but if a step was necessary, to step with their left foot. This was done to ensure steps would be reactive and not voluntary, intentional steps. Two blocks of ramp and hold perturbations in each of these 12 directions were presented. In the stepping block, the platform's displacement was 23 cm, velocity was 45 cm/s, and acceleration was 0.75 g. In the nonstepping block, the platform's displacement was 12.4 cm, velocity was 35 cm/s, and acceleration was 0.5 g. The perturbation directions were randomized during each block of perturbations to minimize anticipatory adjustments and increase response variability. Due to the influence of prior trials on a subject's response (Horak and Nashner 1986), we first collected the stepping block of trials and then the nonstepping block of trials. Five trials of each condition (stepping and nonstepping) in each of the twelve directions of perturbation were collected. In the stepping condition, all subjects took a step in response to perturbations in all directions.

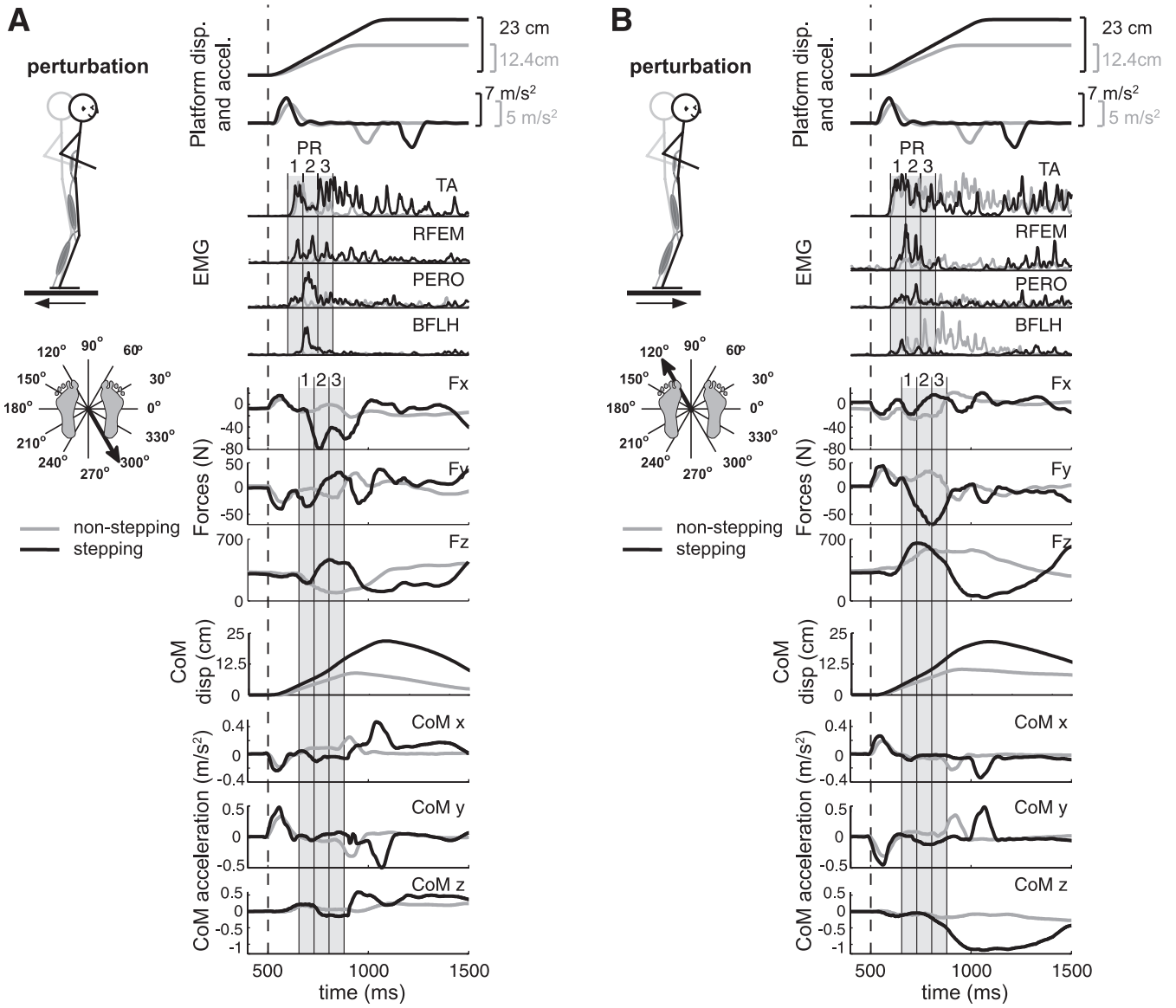


Fig. 1. Example of postural responses to a backward and rightward perturbation of the support surface (*A*) and to a frontward and leftward perturbation of the support surface (*B*). Balance perturbations were induced by ramp and hold perturbations in 12 evenly spaced directions in the horizontal plane. Platform displacement and acceleration profiles used to induce nonstepping (gray) or stepping (black) responses are shown. Electromyographic (EMG) responses occurred ~100 ms after the onset of platform motion (vertical dashed line). Shown here are the tibialis anterior (TA), rectus femoris (RFEM), peroneus (PERO), and biceps femoris long head (BFLH) EMG responses. Mean EMG activity was calculated for three time bins during the automatic postural response (PR), indicated by the shaded region, beginning 100 ms (PR1), 175 ms (PR2), and 250 ms (PR3) after perturbation, as well as one background time period. Ground reaction forces (GRFs) under the right foot as well as center of mass (CoM) position and acceleration are also shown.

Occasionally subjects stepped with their right foot, and these trials were excluded from the analysis. In the nonstepping condition, all subjects maintained balance without taking a step.

Since many muscles are required for the muscle synergy analysis, surface EMG activity was recorded from 16 lower back and leg muscles on the subject's right side, which was the stance leg in stepping responses. The muscles recorded included the following: vastus lateralis (VLAT), rectus femoris (RFEM), rectus abdominis (REAB), biceps femoris long head (BFLH), semitendinosus (SEMT), adductor magnus (ADMG), erector spinae (ERSP), abdominal external oblique (EXOB), vastus medialis (VMED), tibialis anterior (TA), medial gastrocnemius (MGAS), lateral gastrocnemius (LGAS), soleus (SOL), peroneus (PERO), tensor fasciae latae (TFL), and gluteus medius (GMED). EMG data were high-pass filtered at 35 Hz, demeaned, rectified, and low-pass filtered at 40 Hz using custom MATLAB routines. Additionally, kinetic data were collected at 1,080 Hz from force plates under the feet (AMTI, Watertown, MA), and kinematic data were collected at 120 Hz using a motion capture system (Vicon, Centennial, CO) and a custom 25-marker set that included head-arms-trunk and bilateral thigh, shank, and foot segments (Winter 1990). CoM acceleration was calculated from ground reaction forces (GRFs; force = mass × acceleration), and CoM position was calculated using kinematic data and the Vicon Plug-in-Gait model. CoM velocity computed from differentiated marker data matched well with the CoM velocity computed from integrated force data. CoM displacement and velocity were not used in the functional muscle synergy analysis.

Data processing. To account for temporal variations in muscle activity, four time bins were analyzed: one before the perturbation and three during the automatic postural response (APR). The platform moved at 500 ms after the beginning of the trial. A background period beginning 50 ms after we began collecting data and ending 170 ms

before the perturbation onset was analyzed to determine the resting activity of each muscle. The APR has been well characterized and occurs ~100 ms after the perturbation (Horak and Macpherson 1996); due to temporal variations in muscle activity during this APR, we further divided it into three time bins. Each one lasted 75 ms and began 100 ms (PR1), 175 ms (PR2) and 250 ms (PR3) after the perturbation (see Fig. 1, shaded areas). Mean muscle activity for each muscle during each time bin was calculated for each trial. These numbers were assembled to form a data matrix, which consisted of 4 time bins × 12 directions × 5 trials × 2 conditions = 480 points for each of the 16 muscles. For display purposes, each muscle's EMG values were initially normalized to the maximum value across all time periods, perturbation directions, and conditions so that each value was between 0 and 1. Before muscle synergies were extracted, each muscle vector was normalized to have unit variance to ensure equal weighting in the muscle synergy extraction.

Kinetic and kinematic variables were also analyzed to determine whether muscle synergy activations were consistently correlated with a particular behavioral goal. GRFs were rotated such that the vertical forces were aligned with the limb axis (defined by the vector between the hip and ankle markers), as in Torres-Oviedo et al. (2006). The time bins used to consider GRFs were 60 ms after the PR time bins used for EMG data, due to electromechanical delays (Jacobs and Macpherson 1996). Therefore, the time windows for the three PR periods were 160–235, 235–310, and 310–385 ms after the perturbation onset for forces. Background forces were subtracted from the forces in each time period, so the force data represent a change from background. To use non-negative matrix factorization (NNMF; described below), the positive and negative components of the forces were separated, resulting in six additional data rows to be included in the matrix ($Fx+$, $Fx-$, $Fy+$, $Fy-$, $Fz+$, and $Fz-$). Similarly, CoM acceleration data were analyzed the same way as GRF data. CoM acceleration was averaged over three time periods: 160–235, 235–310, and 310–385 ms after the perturbation onset, and background CoM acceleration was subtracted out. The positive and negative components were separated, each row was normalized to the maximum value, and then averaged over the same time periods as were used for GRFs. Each functional variable was added into the data matrix of EMG data for extraction of functional muscle synergies (as described below). As with the EMG data, each row was normalized to have unit variance before functional muscle synergies were extracted to ensure a uniform representation of variance across the data pool. The large passive forces that occur in the vertical force component due to perturbation dynamics and changes in weight bearing were confounding factors. In some perturbation directions (leftward), the vertical forces were mostly passive in the stepping condition, due to the movement of the platform rather than active muscle activation. Because we were primarily interested in the directional control of forces in the horizontal plane due to muscle synergy recruitment, we included only the four components of horizontal-plane force ($Fx+$, $Fx-$, $Fy+$, and $Fy-$) in the muscle synergy analysis.

Extraction of muscle synergies from EMG data. We extracted muscle synergies from the data matrix of EMG recordings using NNMF (Lee and Seung 1999; Tresch et al. 1999), which has previously been used for muscle synergy analysis (Ting and Macpherson 2005; Torres-Oviedo and Ting 2007). This is a linear decomposition technique that assumes that a muscle activation pattern (M) in a given time period that was evoked by a perturbation in a particular direction is composed of a linear combination of a few muscle synergies (W_i) that are each recruited by a synergy recruitment coefficient (c_i). Therefore, a particular muscle activation pattern at a particular time in response to a particular perturbation would be represented by the following:

$$M = c_1W_1 + c_2W_2 + c_3W_3 + \ldots$$

W_i specifies the muscles involved in synergy i and their relative contributions. Each component of W_i represents the contribution of one particular muscle to that synergy, and an individual muscle may contribute to multiple synergies. The muscle synergies do not change composition across conditions, and each one is multiplied by a scalar recruitment coefficient (c_i), which changes over time and across conditions. c_i has been hypothesized to represent the neural command that specifies how that synergy is modulated over time and how much each synergy will contribute to a muscle's total activity pattern (Ting 2007). After functional muscle synergies were extracted, the unit variance scaling was removed from data so that each muscle, kinetic, and kinematic variable ranged from 0 to 1 to permit data inspection and interpretation.

To select the number of muscle synergies that could best reproduce our data, we extracted 1–16 synergies from 60% of the nonstepping trials for each subject and used these to reconstruct the EMG data from the remaining nonstepping trials (for cross-validation) and from the stepping trials. These were termed "shared" muscle synergies. We selected the fewest number of shared muscle synergies (N_{syn}) that could adequately reconstruct the muscle responses in the nonstepping condition. The goodness of fit of the data reconstruction using these muscle synergies was quantified by the data variability accounted for (VAF), which was defined as 100 × uncentered Pearson's correlation coefficient (Torres-Oviedo et al. 2006; Zar 1999). We selected N_{syn} muscle synergies that accounted for at least 90% of the overall nonstepping data variability (i.e., VAF > 90%). Note that overall VAF was found by calculating VAF for the entire nonstepping data set. Moreover, we also had a local criterion in which N_{syn} accounted for at least 75% of the data variability in each muscle and each condition. Muscle VAF and condition VAF were calculated by considering only a portion of the nonstepping data set. Muscle VAF for each muscle quantified the extent to which the muscle synergies accounted for variability in the activity of individual muscles across all time bins, perturbation directions, and trials. Condition VAF for each perturbation direction quantified the extent to which the muscle synergies accounted for the variability in muscle activation patterns formed by the response of all 16 muscles to a single perturbation direction during 1 time bin across all 5 trials. This local fit criterion was more stringent and ensured that relevant features of the data set were reproduced. The number of muscle synergies was increased until they could account for >75% muscle VAF in each muscle and for >75% condition VAF in each perturbation direction and further increased if local fits were improved. However, if an additional muscle synergy contributed evenly to the VAF across muscles and perturbation directions, it was not included because it likely represented noise in the data rather than variations due to trial or perturbation direction. N_{syn} was also validated using factor analysis: 1–16 factors were extracted, and the log likelihood of each was plotted versus number of factors. N_{syn} was chosen by finding the point on the log likelihood curve where curvature is greatest (Tresch et al. 2006).

To validate N_{syn} we compared the overall VAF using the identified muscle synergies to the overall VAF using muscle synergies extracted from shuffled data. We estimated 95% bootstrap confidence intervals (CIs) for the overall VAF when using 1–16 muscle synergies extracted from the original data and 1–16 muscle synergies extracted from a shuffled data set. We used bootstrapping with replacement (Cheung et al. 2009a; Efron 1993) to resample each data matrix. The overall VAF due to reconstruction by either the 1–16 muscle synergies extracted from the original data or the 1–16 muscle synergies selected from shuffled data was calculated for 500 resampled datasets to generate CIs. VAF values were sorted, and 95% CI bounds were estimated by selecting the 2.5 and 97.5 percentiles of the VAF distribution. In the shuffled version of the original data matrix, each muscle's data were shuffled independently; therefore, this shuffled data matrix contained the same values, range, and variance for each muscle, but the relationships between muscle activations were removed. The VAF CI found using the muscle synergies extracted from the original data set was compared with the VAF CI found using muscle synergies from the shuffled data.

"Stepping-specific" muscle synergies were extracted from stepping data that was not accounted for by the shared muscle synergies described above. To this end, we used an iterative algorithm that held fixed the shared muscle synergies extracted from nonstepping data while optimizing a new set of muscle synergies, termed "stepping specific," extracted from the remainder of the variability in the stepping data not accounted for by the shared muscle synergies (Cheung et al. 2009a; Torres-Oviedo and Ting 2010). In this iterative process, the recruitment coefficients of shared and stepping-specific muscle synergies were also optimized. We extracted one to five stepping-specific muscle synergies and selected the fewest number of muscle synergies (shared and specific) that could adequately reconstruct the stepping responses, as measured by VAF $>$ 90% of the overall data and $>$75% of the muscle and condition VAF (described above). Moreover, to validate the shared and stepping-specific muscle synergies, we compared them with muscle synergies extracted from data in both conditions (i.e., nonstepping and stepping) and from data in each condition alone. The quantification of similarity between muscle synergy sets is described in *Data analysis*.

Extraction of functional muscle synergies from EMG, forces, and CoM acceleration. To determine if the muscle synergy activations were related to a particular biomechanical function or behavioral goal, we extracted 1–16 functional muscle synergies from a data matrix of nonstepping trials that contained muscle activity as well as forces under the feet and CoM acceleration (forces and CoM acceleration were lagged 60 ms behind EMG, as discussed above). Because we used NNMF to extract muscle synergies, all of the input data needed to be positive; therefore, positive and negative components of force and CoM acceleration were separated as previously described. Functional muscle synergies were extracted from nonstepping data first and then used to reconstruct the stepping data. If necessary, stepping-specific functional muscle synergies were also extracted. As a validation, functional muscle synergies were also extracted from EMG and force data without CoM acceleration data and from EMG and CoM acceleration data without force data included.

Data analysis. Once N_{syn} and an appropriate number of stepping-specific functional muscle synergies (if needed) were selected, the functional muscle synergies were used to reconstruct the EMG, force, and CoM acceleration patterns for the stepping and nonstepping trials. Measured data and reconstructed data were compared for a particular muscle, force, CoM acceleration component, or perturbation direction for each of the five trials to examine the ability of the synergies to account for intertrial variations. Similarity between measured and reconstructed data was quantified using r^2 and VAF (Torres-Oviedo et al. 2006; Zar 1999). We also examined whether the functional muscle synergies could account for temporal and spatial variations in muscle activation, force, and CoM acceleration patterns.

Similarity between two different sets of muscle synergies was determined by calculating correlation coefficients (r) between each muscle synergy vector in the first set and each in the second set. A pair of muscle synergies was considered "similar" if they had $r > 0.623$, which corresponds to the critical value of r^2 for 16 muscles at $P = 0.01$ ($r^2 = 0.388$). An additional analysis was performed to ensure that the muscle synergy "matches" we selected were more similar than would be expected by chance. We calculated the expected mean r and SD based on comparing the first set of muscle synergies with 22,000 random permutations of the elements of the second set of muscle synergies. We transformed the r values between our actual synergy comparison to the standard normal variable (Z) using the following equation: $Z = X - \mu/\sigma$, where X is the r value between one synergy in the first set and one in the second set, μ is the mean r, and σ is SD. An r of $>$0.623 corresponds to a Z score of $>$2.409, indicating the pair of muscle synergies is statistically more similar than would be expected by chance ($P < 0.008$). All of the muscle synergy pairs that we call "similar" met this criterion.

RESULTS

For all subjects, a few muscle synergies reproduced both stepping and nonstepping responses to multidirectional balance perturbations, accounting for temporal, spatial, and intertrial variability in muscle activation patterns as well as task-level variables such as GRF and CoM acceleration. Different patterns of muscle activity were observed in these two very different tasks, resulting in variations in muscle tuning. Common muscle synergies in the stance leg were used in both nonstepping and stepping responses. In stepping responses, one additional stepping-specific muscle synergy was required in all subjects, perhaps providing stabilization to the stance limb to swing the stepping limb forward. Furthermore, functional muscle synergies (which included forces and CoM accelerations) were able to account for force direction and CoM acceleration direction in both nonstepping and stepping responses.

Nonstepping versus stepping responses. In all subjects, after perturbations, CoM movement and forces under the stance foot were initially similar in both behaviors (PR1) but diverged in PR2 or PR3 in stepping versus nonstepping behaviors. For example, forces during a 300° perturbation were initially similar in stepping and nonstepping (Fig. 1, PR1). In both conditions, the right leg was initially unloaded in PR1 as a result of the perturbation. In nonstepping behaviors, the right limb was slowly loaded again after PR3 as the subject regained balance (Fig. 1). However, in stepping responses, the right limb was rapidly loaded during PR2 so that the subject could take a step with the left leg, and the right leg was then slowly unloaded as body weight was redistributed onto both legs after PR3 (Fig. 1, compare PR1 with PR3). Similarly, for all subjects, the CoM was initially accelerated and displaced away from the feet in both stepping and nonstepping responses to balance perturbations (e.g., Fig. 2). However, in stepping responses, the CoM continued moving in the same direction away from the feet in the later time periods (PR2 and PR3), whereas in nonstepping responses, the CoM was accelerated in the opposite direction returning the CoM back above the feet during PR2 and PR3 (Fig. 1).

Likewise, after perturbations, EMG activity was initially similar in the two behaviors (PR1) but diverged at later time points depending on which behavior was used (Fig. 1). The latencies to muscle onset and initial muscle activation patterns (PR1) were similar in both nonstepping and stepping responses. The latency to step initiation ranged from 130 to 280 ms after the perturbation onset. Across all perturbation directions, muscles had the same tuning in both behaviors during PR1 (Fig. 3). The tuning directions in nonstepping responses stayed the same throughout the postural response. However, in stepping responses, the muscle tunings were dramatically different by PR3. For example, during PR3, PERO was most active during stepping responses for rightward lateral perturbations, whereas it was most active for leftward lateral perturbations during nonstepping responses (Fig. 3, PR3). Likewise, SOL was most active in stepping responses for leftward, forward perturbations, but in nonstepping responses it was most active for leftward, backward perturbations in PR3.

Muscle synergies were shared between nonstepping and stepping responses. In nonstepping postural responses, 4–6 muscle synergies/subject were sufficient to account for $>$90% total variability and $>$75% variability in each muscle and

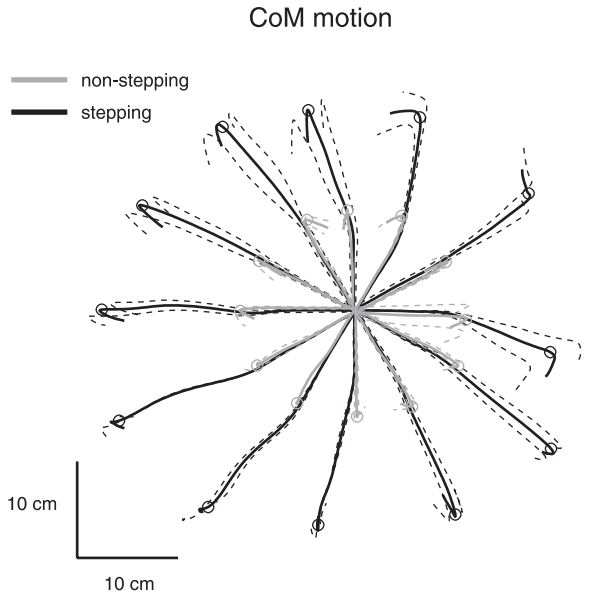


Fig. 2. CoM displacement during nonstepping (gray) and stepping (black) responses to perturbations from 500 ms before the perturbation until 150 ms after the platform stopped moving. Shown are the mean and SD for the five trials in each direction for one subject. The open circle at the hook of each trace marks the point at which the platform stopped moving. In both conditions, the CoM was initially displaced 10–12 cm in the direction opposite the platform movement. In nonstepping responses, the CoM then moved back toward the starting position, whereas in stepping responses, the CoM continued moving away from the starting position as the subject took a step.

condition (all 4 time bins, 12 perturbation directions, and 5 trials of each) in the EMG data. These values were several CIs higher than would be expected by chance. CIs for VAF of extracted muscle synergies did not overlap with VAF CIs of muscle synergies extracted from shuffled data except for the case where only one muscle synergy was extracted (Fig. 4*A*, *subject 1*). Five muscle synergies were selected for *subject 1*, and the VAF CI confirmed this selection since this was the lowest number of muscle synergies required for the upper bound of the CI to exceed 90% VAF (Cheung et al. 2009a) The lower bound of the VAF CI for five muscle synergies was 2.45 CIs above the VAF CI for five muscle synergies extracted from shuffled data (Fig. 4*A*). Across subjects, the lower bound of the VAF CI for the selected number of muscle synergies (4–6 muscle synergies/subject) was 2.51 ± 0.79 CIs above the same number of muscle synergies extracted from shuffled source data.

Several analyses demonstrated that muscle synergies used in the stance leg were shared between stepping and nonstepping responses. Figure 4*B* shows the results for one of the multiple comparisons performed between muscle synergy sets in a sample subject. Muscle synergies extracted from nonstepping data were shuffled 22,000 times and compared with muscle synergies extracted from stepping to generate a distribution of r values expected by chance (Fig. 4*B*). Note that the r values that result when comparing muscle synergies extracted from the nonstepping data with those extracted from the stepping data fall beyond the threshold of r values expected by chance ($r > 0.623$, corresponding to a Z score of >2.409; Fig. 4*B*). Four of the five muscle synergies extracted from nonstepping in *subject 1* were similar to four of the five muscle synergies extracted from stepping in the same subject ($r > 0.74$; Fig. 4*B*). The distribution of Z scores for the r values between all muscle synergies extracted from stepping and nonstepping was bimodal, with the muscle synergies considered to be similar clustered toward the upper end of the distribution. Across subjects, in stepping responses, five to seven muscle synergies were required; four to six of the stepping muscle synergies were similar to those from nonstepping, and there was one additional muscle synergy used only during stepping responses. Furthermore, when muscle synergies were extracted from a data matrix containing both nonstepping and stepping trials, similar muscle synergies were identified (Fig. 4*C*). Four

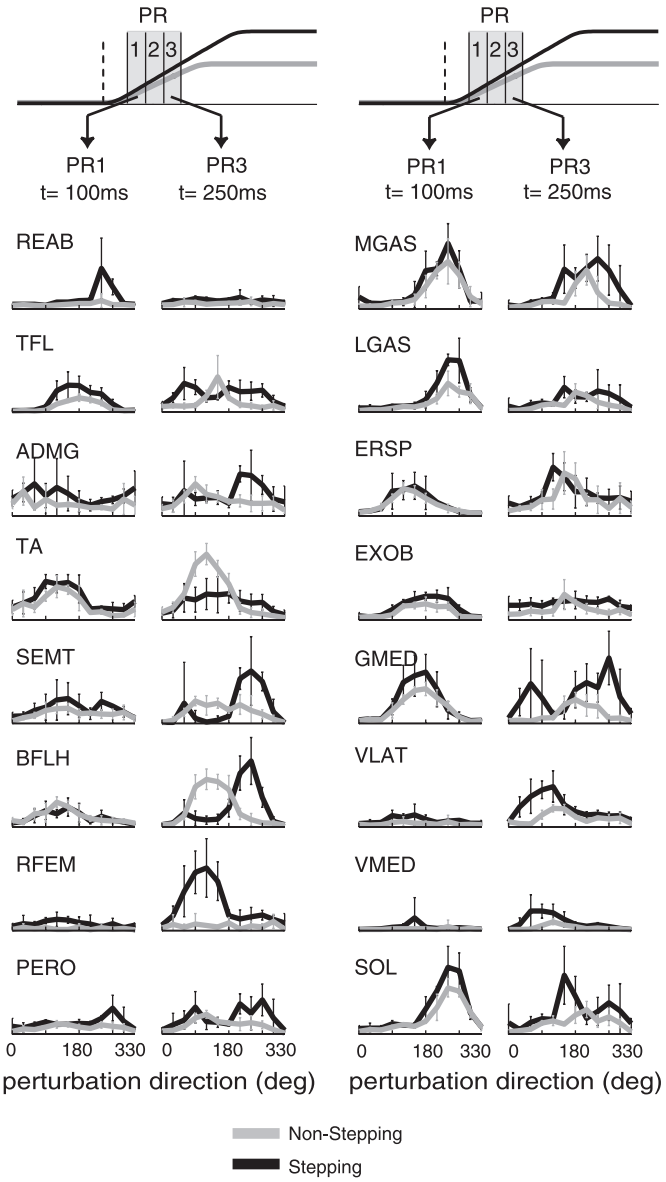
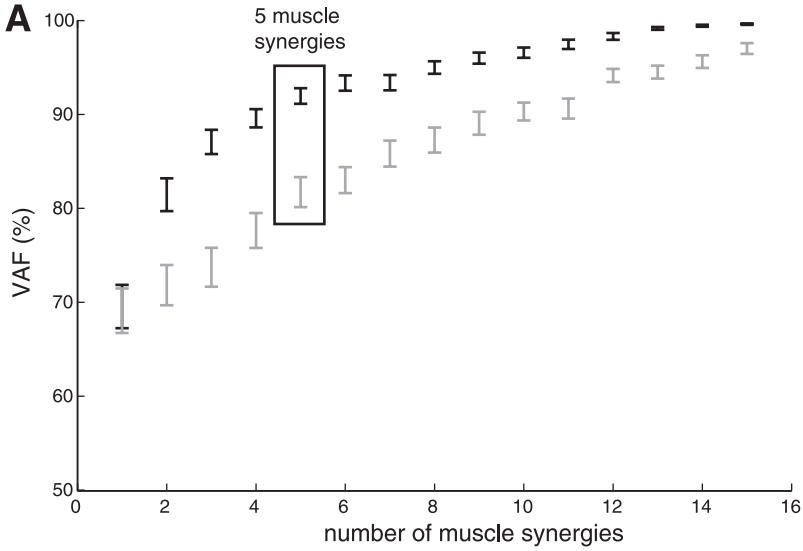
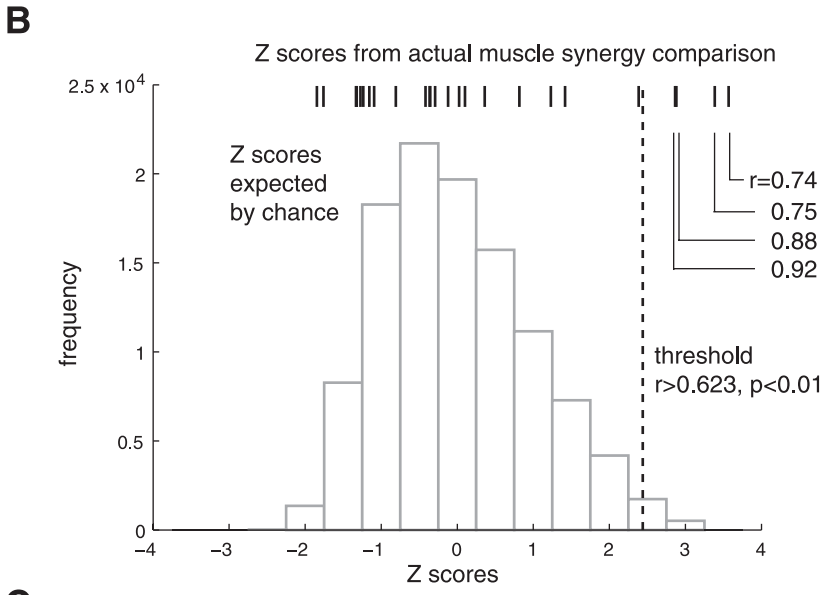


Fig. 3. Muscle tuning curves for all 16 muscles during nonstepping (gray) and stepping (black) responses during time windows PR1 and PR3 for a representative subject. Muscle tuning curves varied in magnitude over all perturbation directions, and their shapes varied from muscle to muscle, over time, and between nonstepping and stepping responses. Shown are the mean tuning curves ± SD for five trials in each perturbation direction, presented randomly. The muscles recorded included the following: vastus lateralis (VLAT), RFEM, rectus abdominis (REAB), BFLH, semitendinosus (SEMT), adductor magnus (ADMG), erector spinae (ERSP), abdominal external oblique (EXOB), vastus medialis (VMED), TA, medial gastrocnemius (MGAS), lateral gastrocnemius (LGAS), soleus (SOL), PERO, tensor fasciae latae (TFL), and gluteus medius (GMED).





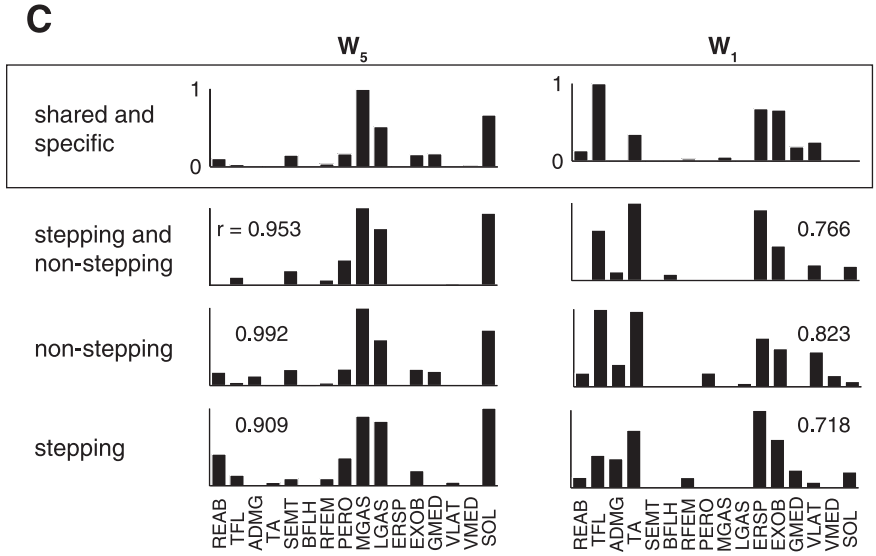


Fig. 4. *A*: 95% confidence intervals (CI) of the reconstruction variability accounted for (VAF) estimated using bootstrapping (black lines) and 95% CIs of the reconstruction VAF when muscle synergies were extracted from a shuffled matrix of the same data (gray lines). For *subject 1* (shown here), five muscle synergies were selected, and the lower bound of the VAF CI for five muscle synergies was 2.45 CIs above the VAF CI for five muscle synergies extracted from shuffled data. *B*: demonstration of the criteria used to quantify muscle synergy similarity. Muscle synergies extracted from shuffled nonstepping data were compared with muscle synergies extracted from stepping to generate a distribution of *Z* scores for how similar two muscle synergies are predicted to be based on chance (gray histogram). The *Z* scores for the comparisons between the actual muscle synergies from nonstepping and the muscle synergies from stepping are shown as black vertical lines. A pair of muscle synergies was considered "similar" if $r > 0.623$, corresponding to a *Z* score of >2.409 (dotted vertical line). For *subject 1*, four of the five muscle synergies extracted from nonstepping were similar to four of the five muscle synergies extracted from stepping. *C*: comparison of muscle synergies extracted from various combinations of data. Shown are two muscle synergies, W_5 and W_1, from a representative subject. The "shared and specific" image shows muscle synergies extracted from 60% of nonstepping trials and used to reconstruct the remaining nonstepping data as well as stepping responses. This was the final processing method selected, and these are the muscle synergies shown in Fig. 5. All other extracted muscle synergies were compared with these. The "stepping and nonstepping" image shows muscle synergies identified from all of the nonstepping and stepping data combined into one large data matrix. Shown are *r* values from comparing these vectors with those identified using the shared/specific algorithm. The "nonstepping" image shows muscle synergies extracted from all of the nonstepping data only. The "stepping" image shows muscle synergies extracted from all of the stepping data only. Extracted muscle synergies were similar regardless of the data sets used for analysis, suggesting that they were conserved across conditions.

muscle synergies were found to be similar across all four different extractions using different data pools (Fig. 4*C*). To illustrate the range of fits, Fig. 4*C* shows examples of a muscle synergy that was very similar across extractions (W_5) and another muscle synergy that had relatively low r values but was still considered similar (W_1).

Therefore, for the rest of our analyses, muscle synergies were extracted from 60% of nonstepping trials (shared synergies) and used to reconstruct the remaining nonstepping trials (cross-validation) as well as the stepping data. The shared muscle synergies could account for 93 ± 1% of the overall variability (VAF between EMG and reconstruction for the entire data set) and 79 ± 7% variability across muscles and conditions in the nonstepping behavior (average VAF for individual muscles and conditions across all subjects). These shared muscle synergies also could account for 85 ± 3% of the overall variability and 72 ± 7% variability across muscles and conditions in the stepping behavior. With the addition of one extra stepping-specific muscle synergy, the overall VAF was increased to 91 ± 2% in stepping and 81 ± 4% variability across muscles and conditions. For all subjects, these muscle synergies were similar to those extracted from each behavior individually and together (r = 0.83 ± 0.10; Fig. 4*C*). The compositions of the shared muscle synergies were similar to those found previously during nonstepping postural responses (Torres-Oviedo and Ting 2007) and were composed of muscles spanning multiple joints (Fig. 5). In each subject, there was an additional muscle synergy used in stepping that was not found in nonstepping responses, which was typically composed of the vasti and RFEM as well as GMED, a muscle important in walking. It was strongly activated for forward perturbations (in which the subject takes a step backward), perhaps providing forces to stabilize the stance limb or push the swing leg backward.

Muscle synergy recruitment tuning curves explain individual muscle differences in nonstepping and stepping responses. In all subjects, the muscle synergy tuning curves initially had similar tuning directions (PR1 and PR2) but later (PR3) changed tuning direction if a stepping behavior was selected. Similar to individual muscle tuning, muscle synergy tuning with respect to perturbation direction was maintained across all three time bins during nonstepping responses (Fig. 5, gray curves) but changed by PR3 in stepping responses (Fig. 5, colored curves). In this subject as well as the others, each muscle synergy had the same tuning in PR1 and PR2 in both nonstepping and stepping responses. In nonstepping responses, this same tuning was maintained in PR3, whereas for stepping responses, the tuning of some of the muscle synergies changed. For example, W_3 (Fig. 5, red), comprised mainly of TA and quadriceps muscles, was recruited in forward perturbations in PR1 and PR2 in both stepping and nonstepping responses as well as PR3 in nonstepping, as the subject had fallen backward and was trying to pull their body forward to restore balance. In PR3 in stepping responses, however, W_3 was recruited much less, as the subject had switched behaviors and had begun to take a step backward. Instead, the subject used the stepping-

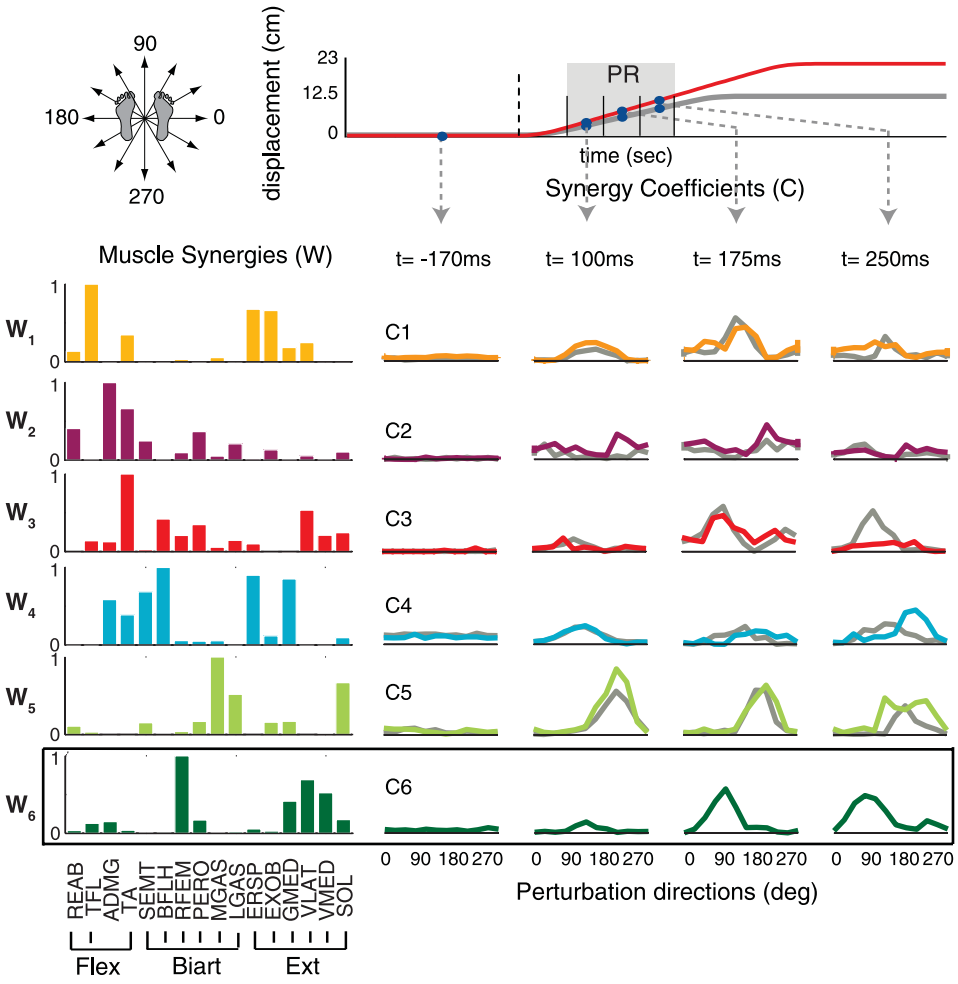


Fig. 5. Muscle synergy vectors (W) and recruitment coefficients (C) for a representative subject. Muscle synergy vectors (W_1–W_5) were extracted from EMG data during nonstepping responses and used to reconstruct stepping responses. W_6 is an additional stepping-specific muscle synergy required to achieve a good reconstruction of stepping responses. Shown are the average muscle synergy recruitment coefficients for five trials in each perturbation direction for both nonstepping responses (gray) and stepping responses (color). Directional tuning of muscle synergies can be observed over the three response time bins as well as differences in muscle synergy recruitment between nonstepping and stepping responses.

specific muscle synergy W_6 (Fig. 5, dark green) in forward perturbations during PR2 and PR3, when the switch had been made to a stepping behavior. During stepping responses, W_4 (Fig. 5, blue) changed from being recruited in forward, leftward perturbations in PR1 to being recruited for backward, leftward perturbations by PR3. These trends were seen in multiple subjects.

The shifts in muscle synergy tuning direction could explain the patterns of muscle activity (and individual muscle tuning curves) observed in both nonstepping and stepping behaviors (comparison between real and reconstructed tuning curves in both nonstepping and stepping: $r^2 = 0.77 \pm 0.24$, VAF = $94 \pm 6\%$; Fig. 6). For example, BFLH changed tuning in PR3 in stepping responses, and it was activated by W_4 (Fig. 6, blue). TA turned off during PR3 in stepping responses, and it was activated by W_3 (Fig. 6, red). VLAT had similar tuning during PR3 in nonstepping and stepping, but was activated by different synergies. In nonstepping, W_3 (Fig. 6, red) was responsible for activating VLAT, whereas in stepping, the stepping-specific muscle synergy W_6 (Fig. 6, green) activated VLAT. Thus, the muscle synergies were able to reproduce changes in muscle activation patterns with both perturbation direction and time.

Linear regression cannot explain relationships between muscle synergies and functional output variables. Examples of scatter plots of muscle synergy activations versus functional variables (force or CoM acceleration components) showed that linear regression was not sufficient to describe the relationships between muscle synergies and functional outputs (Fig. 7*A*). In

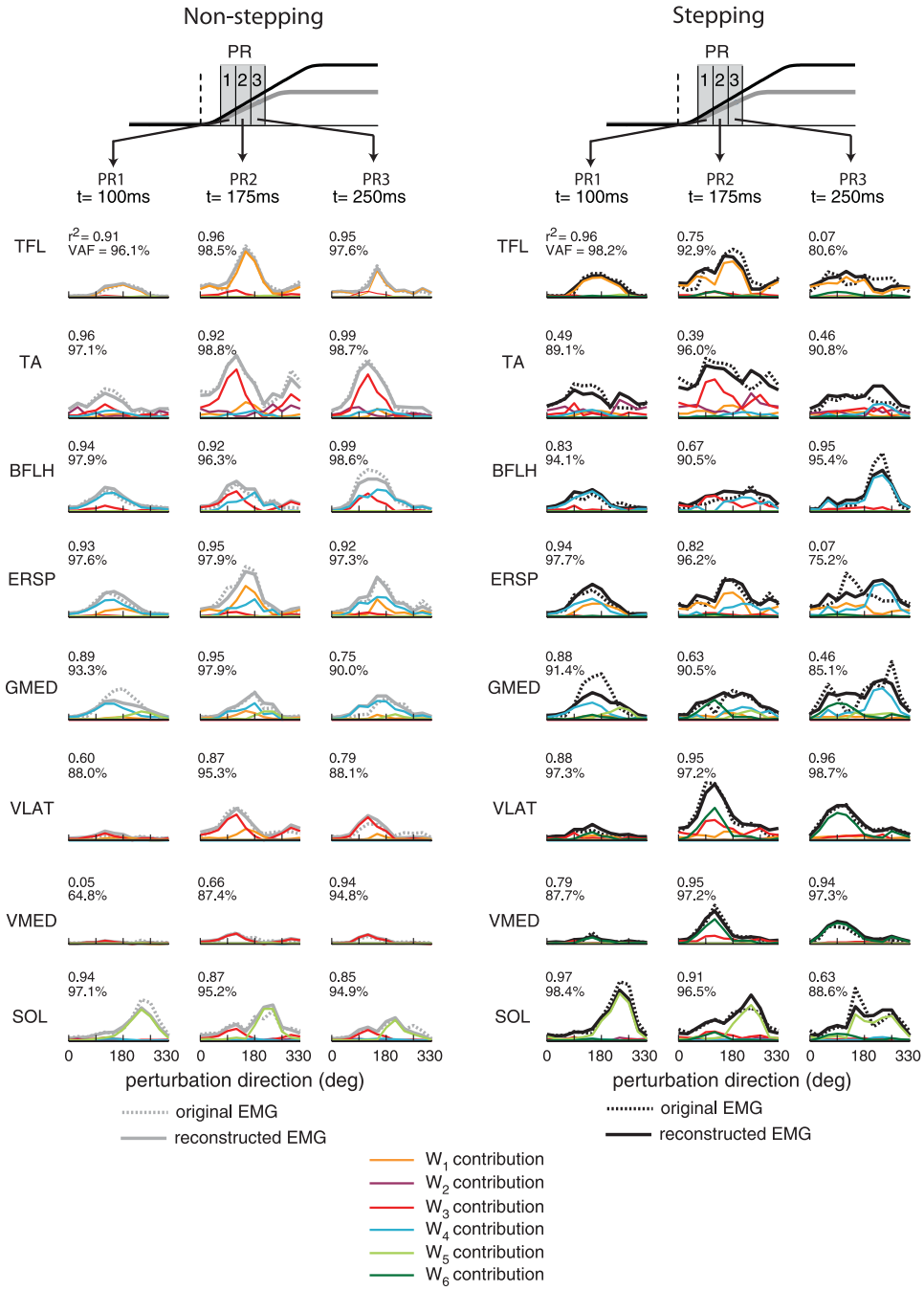


Fig. 6. Reconstructions of the muscle tuning curves using the muscle synergies shown in Fig. 5. Original data are shown by dashed lines and reconstructed data are shown by solid lines (nonstepping in gray and stepping in black). The contribution of each muscle synergy to the reconstruction is shown by the corresponding colored line, all of which were added to generate the total reconstruction. Average r^2 between each muscle tuning curve and the muscle synergy reconstruction was 0.77 ± 0.24, and average VAF between each muscle tuning curve and the muscle synergy reconstruction was $94 \pm 6\%$.

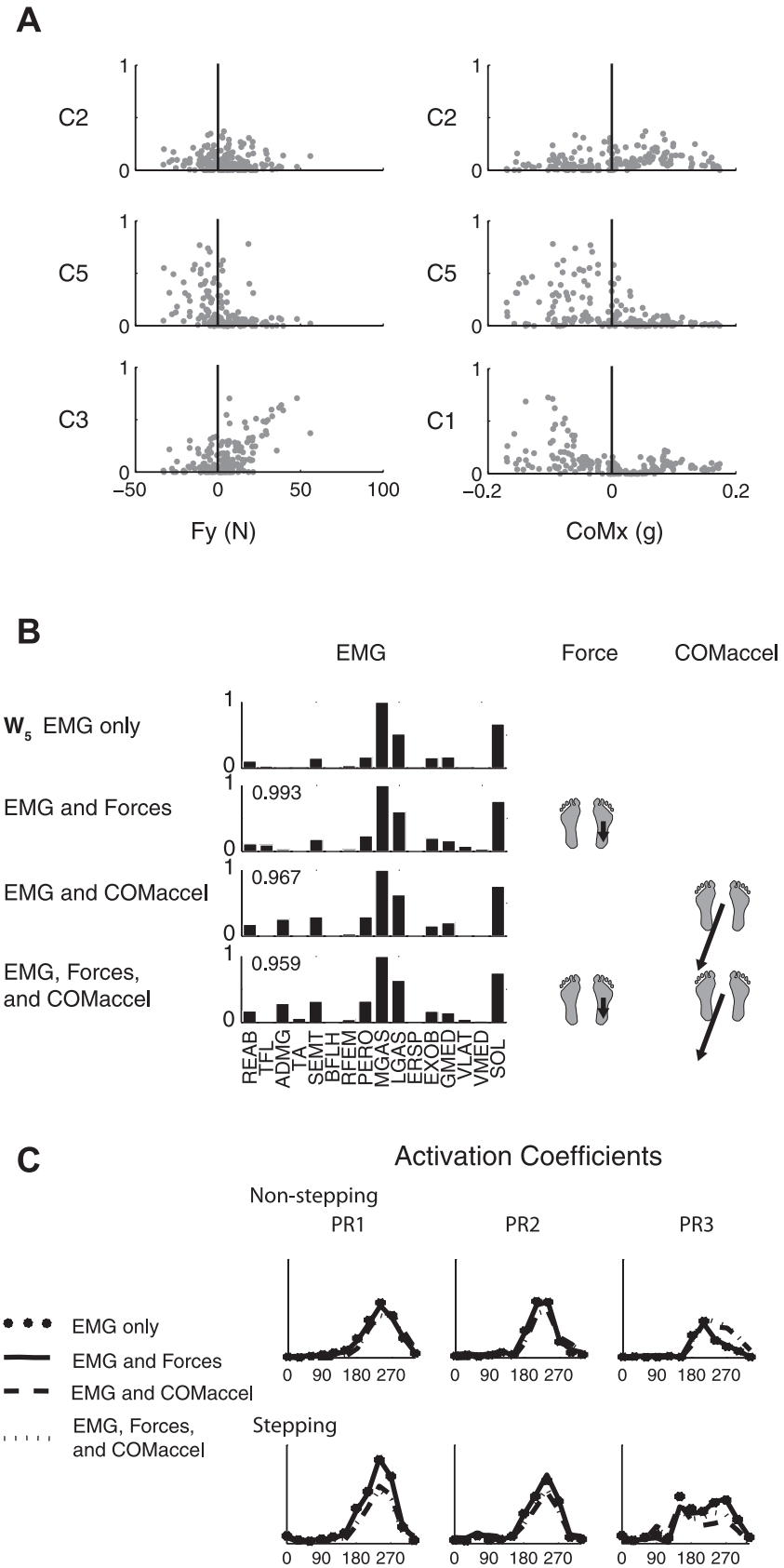


Fig. 7. *A*: example scatterplots of muscle synergy activations versus functional variables (force or CoM acceleration components). C_2 plotted against *Fy* and CoM*x* indicated no relationship between recruiting W_2 and changes in *Fy* or CoM*x*. However, C_5 versus *Fy* revealed a possible relationship between C_5 and *Fy*−, and C_5 versus CoM*x* revealed a possible relationship between C_5 and CoM*x*−. Therefore, functional variables (force and CoM acceleration) were divided into positive and negative components and included in the muscle synergy analysis. *B*: comparison of functional muscle synergies extracted from various combinations of data for a representative subject. Functional variables such as applied forces at the ground and CoM acceleration taken from time windows 60 ms after the EMG time windows were included in the analysis, and functional muscle synergies were identified. Including the functional variables did not change the composition or recruitment of the identified EMG muscle synergies (*r* values comparing the muscle synergy vectors are shown). Comparisons of the muscle synergy vector W_5 extracted from EMG data only (*1*), EMG and force data (*2*), EMG and CoM acceleration data (*3*), and EMG, force, and CoM data (*4*) are shown. Shown are the EMG portions of each of the functional muscle synergies, which were not changed by including the functional variables, as well as the force and CoM acceleration vectors identified from each extraction. *C*: muscle synergy recruitment tuning curves from each of the aforementioned combinations of data. Including the functional variables did not affect the muscle synergy tuning, validating that those forces and CoM accelerations are consistently produced 60 ms after that muscle synergy is recruited.

some cases, there appeared to be no relationship between an individual synergy recruitment coefficient and an individual functional variable, e.g., Fig. 7*A*, C_2 vs. *Fy* (anterior/posterior force) and medial/lateral CoM acceleration (CoM*x*). In many instances, there were discontinuities in the plots at zero crossings of the biomechanical variable, showing that each muscle synergy was correlated to unidirectional changes in the functional variables. For example, there was no apparent relationship between C_5 and *Fy*+ but a possible linear relationship between C_5 and *Fy*− (Fig. 7*A*). Likewise, C_5 also appeared correlated with CoM*x*− but had no relationship to CoM*x*+, demonstrating the same muscle synergy may influence multiple functional variables. Furthermore, C_1 was also correlated with CoM*x*−, demonstrating that more than one muscle synergy may influence the same functional output variable. Inspection of the data thus revealed that there were no clear one-to-one relationships between muscle synergy activations and biomechanical output variables but that there were many partial correlations to unidirectional variations. To better identify causal relationships between muscle synergy activation and functional variables, we divided the functional variables into positive and negative components, increasing the dimension of the biomechanical data, and appended them to the EMG data matrix. We then applied NNMF to the combined data matrix to identify the complex relationships between muscle activity and functional variables.

Functional muscle synergies reveal correlations between muscle synergies and task-level goals. The composition and tuning of the muscle synergies within each subject were not changed by including force and CoM acceleration in the analysis, illustrating that force and CoM acceleration tuning curves were well correlated with muscle synergy tuning curves (Fig. 7, *B* and *C*). For all subjects, the muscle synergy composition was preserved when muscle synergies were extracted from EMGs and forces only, EMGs and CoM acceleration only, as well as EMGs, forces, and CoM acceleration together ($r = 0.83 \pm 0.12$). Similarly, the muscle synergy tuning curves were conserved when the functional variables were included in the analysis. Because of the similarities in functional muscle synergies observed when extracting functional muscle synergies from nonstepping or stepping responses individually, we used the same approach here as we had used to identify muscle synergies: functional muscle synergies were extracted from the nonstepping data and used to reconstruct the stepping data.

Each functional muscle synergy was composed of specific vectors of EMG, force at the ground, and CoM acceleration (Fig. 8). Because the forces and CoM acceleration values we included were delayed 60 ms after the EMG values, we presumed that they were the result of recruiting that muscle synergy. For example, in 90° perturbations, the body initially fell backward, and then in nonstepping responses, the appro-

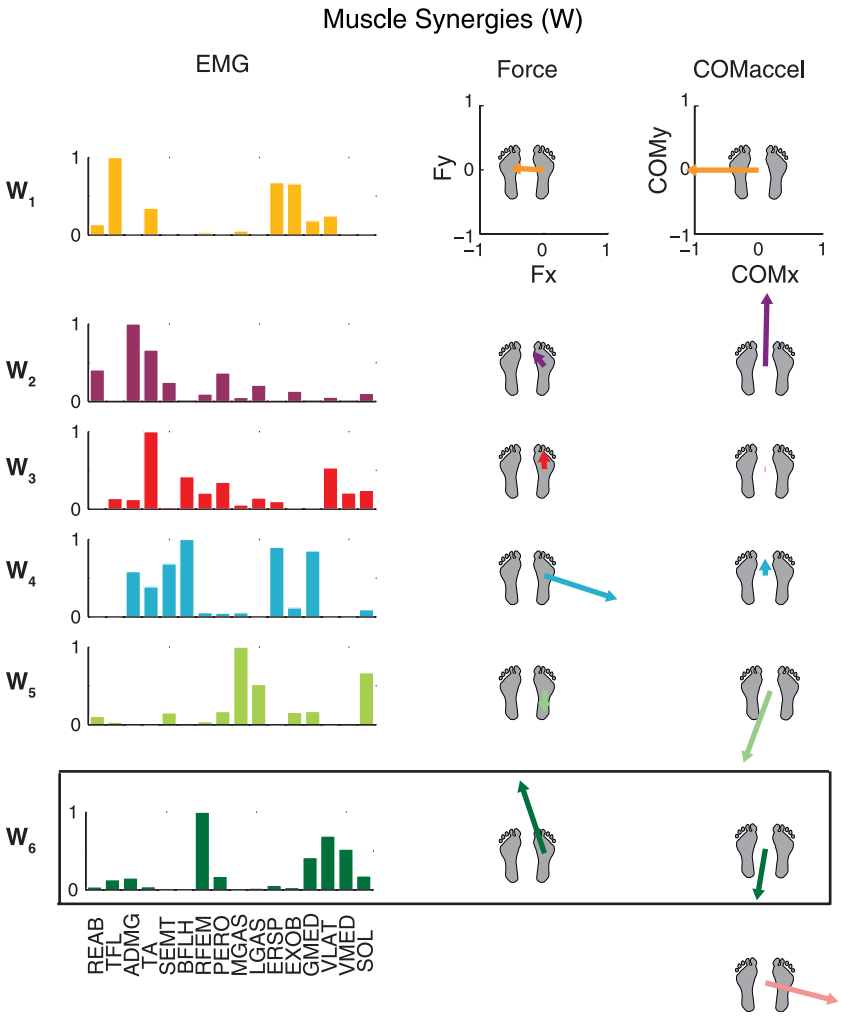


Fig. 8. Functional muscle synergies for a representative subject. Functional variables such as applied forces at the ground and CoM acceleration taken from time windows 60 ms after the EMG time windows were included in the analysis, and functional muscle synergies were identified. Shown are the muscle synergies along with the force and CoM acceleration vector associated with each muscle synergy. The pink CoM acceleration trace is a component identified by the functional muscle synergy analysis that is not attributable to muscle activity in the stance leg.

priate muscles were activated to produce a force forward (W_3; Fig. 8, red) and accelerate the CoM forward (W_2; Fig. 8, purple) to return the CoM above the feet. However, in stepping responses, in PR3, W_3 (Fig. 8, red) was turned off and W_6 (Fig. 8, dark green) was instead recruited, consistent with producing a force forward and accelerating the CoM backward as the subject stepped backward. One extra functional muscle synergy was required when CoM acceleration is included, comprised only of rightward CoM acceleration, tuned for rightward perturbations, presumably correlated to activity in the other leg, since no muscle synergies in the stance leg were activated for that perturbation direction.

The functional muscle synergies containing EMGs and biomechanical variables explained variations in EMG, force direction, and CoM acceleration data in both behaviors. EMGs and CoM accelerations were well reconstructed for both nonstepping and stepping responses in terms of both direction and magnitude using the functional muscle synergies ($r^2 = 0.77 \pm 0.24$, VAF = 91 ± 11%; Fig. 9). The forces during stepping responses that were predicted by the functional muscle synergies from nonstepping were in the appropriate directions, but some of the magnitudes were underpredicted ($r^2 = 0.70 \pm 0.12$, VAF = 68 ± 2%), perhaps due to the much larger forces involved when the other leg was lifted off the ground. The r^2 for force reconstructions was comparable with those of EMG and COM reconstructions, but the VAF for force reconstructions was much lower, indicating the force tuning curve shapes were well reconstructed by the muscle synergies, but the magnitudes were not predicted as well. Functional muscle synergies extracted from stepping alone contained larger forces in the same direction as in nonstepping, which may have been due to the different loading conditions in stepping.

Similar muscle synergies were found across subjects. In general, the muscle synergies were robust across subjects. Different subjects had different numbers of muscle synergies, but there were commonalities in composition and tuning of muscle synergies across subjects. W_5 was similar across all eight subjects ($r = 0.74 \pm 0.07$) and W_4 was similar across seven of eight subjects ($r = 0.82 \pm 0.06$). The muscle synergies also performed similar functions, as evidenced by the muscle synergy recruitment tuning curves (Fig. 10). The subject without W_4 used a different muscle synergy to respond to perturbations in the same direction as W_4, as illustrated by the similarity in the tuning curves of the subject's muscle synergy and that of W_4 in the other subjects. W_3 was another shared synergy similar across six subjects ($r = 0.75 \pm 0.05$), and W_1 was similar across four subjects ($r = 0.75 \pm 0.10$); the remaining subject had different muscle synergies with similar directional tuning. A few other muscle synergies were unique to individual subjects. Additionally, the stepping-specific muscle synergy W_6, found in five of the eight subjects, was similar across subjects ($r = 0.67 \pm 0.05$) and was recruited for the same perturbation directions.

DISCUSSION

Our results suggest that muscle synergies reflect the neural organization of the motor system, representing motor modules recruited to achieve a common biomechanical function across different postural behaviors. We observed that the same muscle synergies were recruited during postural behaviors with different movement dynamics (stepping and nonstepping), but, most importantly, their recruitment was determined by the desired direction of CoM motion and not by the perturbation direction. These results demonstrate that the identified muscle synergies do not simply reflect somatosensory patterns triggering the responses but rather motor modules flexibly recruited to produce biomechanical functions required to stabilize the CoM. Therefore, our results suggest there are separate sensory and motor transformations used by the nervous system to interpret sensory inflow and to construct motor outputs. Consistent neural structures may thus be flexibly accessed and differentially recruited during different motor behaviors by breaking motor activities into their component tasks.

We observed diverse postural responses that became increasingly more complex over time, suggesting the involvement of higher neural centers. While the initial long-latency muscular activity (~100 ms) associated with the automatic postural response was similar in stepping and nonstepping responses, patterns of muscle activity diverged after ~200 ms when a stepping strategy was selected. This observation was consistent across multidirectional postural responses, despite the fact that step latencies varied by direction and step type (i.e., lateral vs. crossover steps). We observed lateral and crossover steps in our study due to the constraint that subjects were required to step with the left leg; however, subjects may naturally choose to use crossover steps even when they are not prompted to do so (King and Horak 2008; Perry et al. 2000). Prior studies have also demonstrated similar muscle onset latencies in the same muscles for nonstepping and stepping responses (Burleigh et al. 1994; McIlroy and Maki 1993a), but the changes in the patterns of muscular activity over time were not investigated. Similarly, it has been suggested that stepping responses are triggered only after the failure of a nonstepping postural response (Horak and Nashner 1986), but our data suggest that stepping muscle activity is initiated before significant destabilization of the body occurs (McIlroy and Maki 1993a). Moreover, the initial muscular response latency during stumbling has been shown to be the same (~50ms), even when later muscle activity (~120 ms) corresponding to distinct corrective strategies differ (van der Linden et al. 2007). Long-latency postural response activity at ~100 ms has been demonstrated to be unaffected by cortical pathways (Woollacott and Shumway-Cook 2002) and the concurrent performance of voluntary motor tasks (Trivedi et al. 2010). Only later muscle activity (~150–350 ms) is modified by attentional factors (Woollacott and Shumway-Cook 2002) or secondary motor goals (Trivedi et al. 2010). Thus, the sequence of postural response events after a perturbation may reflect the sequential and increasingly complex influences of nested hierarchy of neural mechanisms (Ting et al. 2009).

Our results suggest muscle synergies represent a common underlying motor structure for postural responses that is independent of specific sensory patterns. We observed the same set of muscle synergies were recruited when the desired CoM acceleration to recover balance was the same in the stepping and nonstepping responses, but the perturbation directions triggering the responses were different. The differences in the timing and spatial organization of individual muscle activity in the stepping and nonstepping responses were largely explained by altering the recruitment of a common set of muscle synergies, with the addition of only a single muscle synergy specific

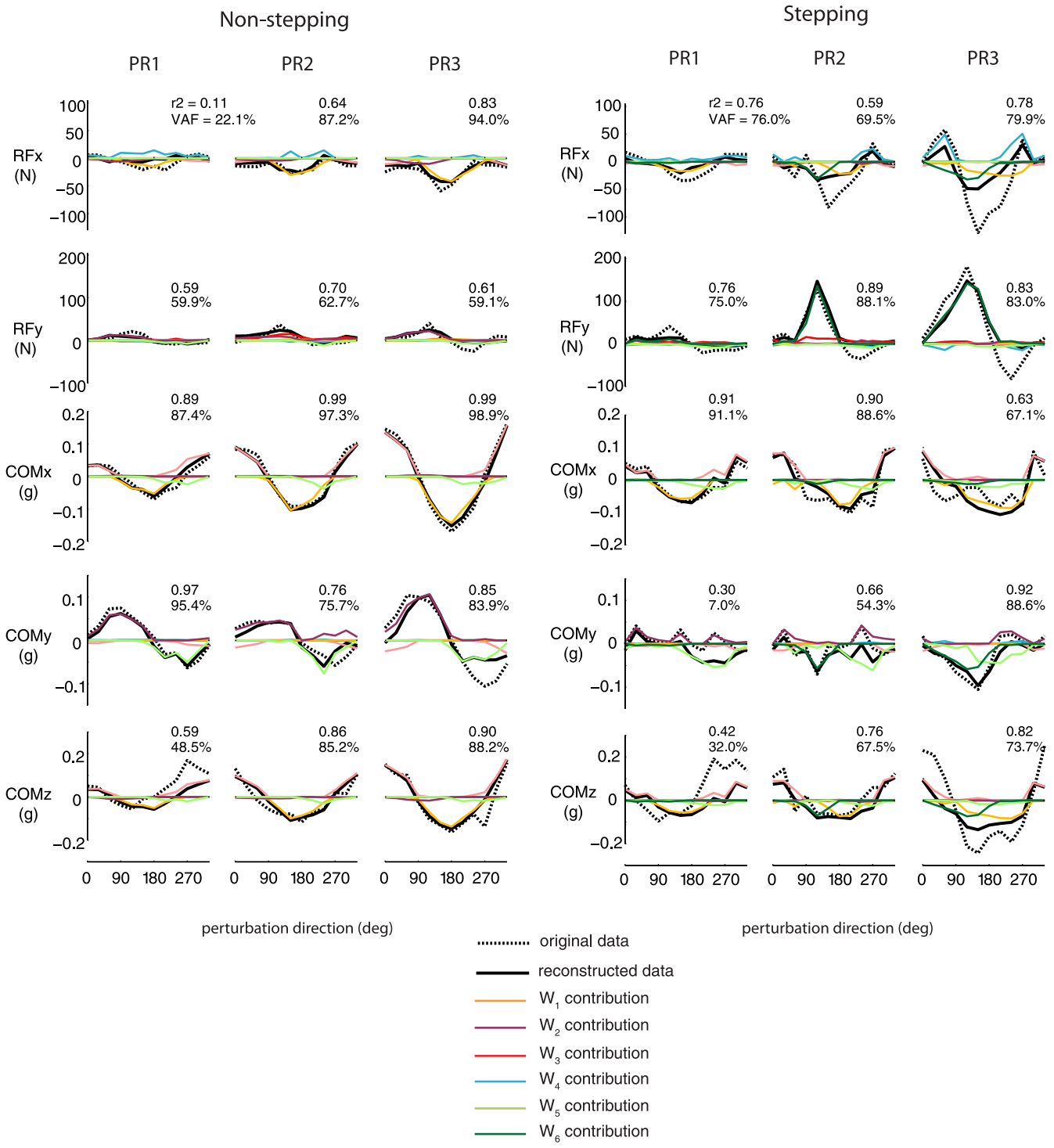


Fig. 9. Reconstructions of the force and CoM acceleration tuning curves using the functional muscle synergies shown in Fig. 8. Original data are shown by dashed lines and reconstructed data are shown by solid lines (nonstepping in gray and stepping in black). The contribution of each muscle synergy to the reconstruction is shown by the corresponding colored line, all of which were added to generate the total reconstruction. Goodness of fit is indicated by r^2 and VAF between each force or CoM acceleration tuning curve and the muscle synergy reconstruction.

to the stepping behavior. Shared and specific muscle synergies have also been demonstrated across different motor behaviors such as frog swimming, kicking, and jumping (Cheung et al. 2009a; Cheung et al. 2005; d'Avella and Bizzi 2005; Hart and Giszter 2004; Kargo and Giszter 2000), human balance control (Torres-Oviedo and Ting 2010), upper limb movements such as reaching (Cheung et al. 2009b; d'Avella et al. 2006; Muceli et al. 2010), and primate hand movements such as grasping (Acharya et al. 2008; Hamed et al. 2007; Overduin et al. 2008). In contrast, a few studies using principal component analysis rather than NNMF have shown that muscle synergies or *m* modes are all reshaped under new conditions (task, time window, etc.) (Danna-Dos-Santos et al. 2007; Robert et al. 2008). The differences in the identified motor modules may

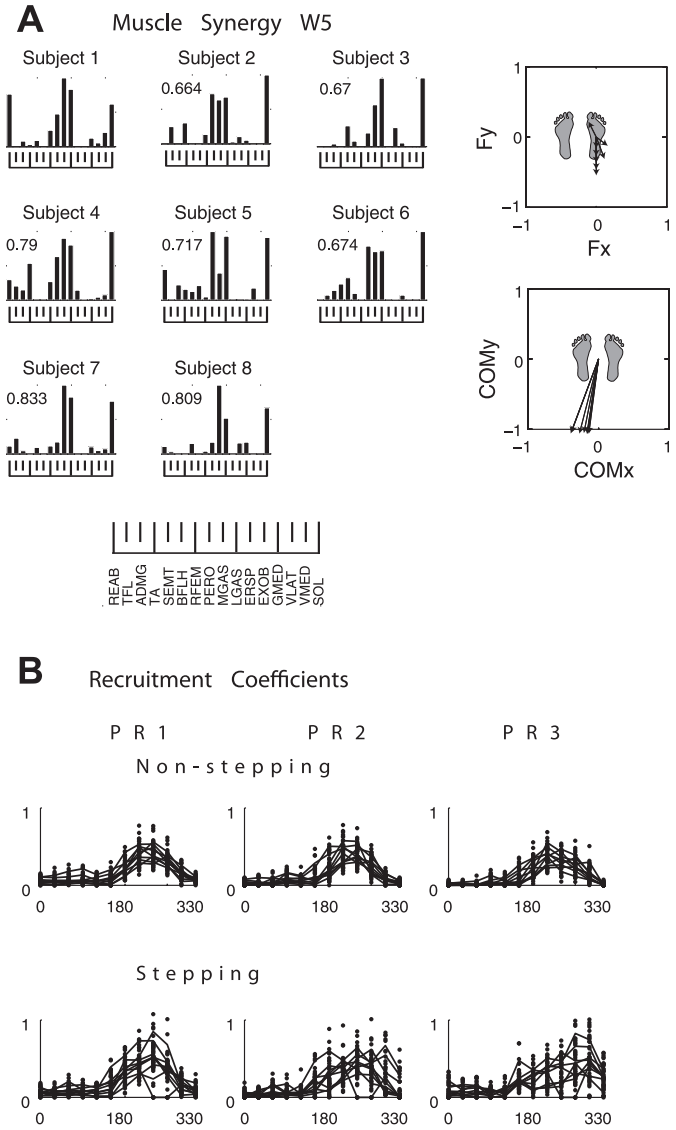


Fig. 10. Comparison of muscle synergy W_5 and its corresponding force vector and CoM acceleration vector (*A*) as well as the corresponding recruitment tuning curve (*B*) across all subjects. One muscle synergy (W_5) was very similar across all subjects, another was similar across seven of the eight subjects (W_4), one was similar across six subjects (W_3), one muscle synergy (W_1) was similar across four subjects, and the remaining muscle synergies were subject specific. In some cases, subjects would use a different muscle synergy to produce a similar force or CoM acceleration, indicating the different strategies people have learned to maintain balance.

reflect a limitation of the chosen decomposition method (Ting and Chvatal 2010; Tresch et al. 2006) or perhaps differences in the type of motor task. Deafferentation studies further support the idea that muscle synergy composition is largely conserved in the absence of somatosensory feedback (Cheung et al. 2005; Giszter et al. 2007; Kargo and Giszter 2000). Moreover, our results suggest muscle synergy recruitment for balance control is determined by task variables such as CoM motion rather than local sensory inputs. This idea is supported by previous studies showing that opposite somatosensory patterns during rotations and translations of the support surface can elicit the same functional muscle synergies to restore balance (Torres-Oviedo et al. 2006). Although somatosensory feedback is essential for the timing of postural responses (Inglis et al. 1994; Stapley et al. 2002), the muscle activity in the initial postural response reflects task variables such as CoM motion (Gollhofer et al. 1989; Nashner and McCollum 1985) rather than simple joint angle changes (Nashner 1977; Ting and Macpherson 2004). Task-level information can be derived from aggregate afferent information in the dorsal root ganglia (Weber et al. 2007) as well as in the dorsospinal cerebellar tract (Bosco et al. 1996). Patterning of the initial postural response is also thought to involve brain stem pathways (Deliagina et al. 2008; Honeycutt et al. 2009; Macpherson et al. 1997). We demonstrated that similar initial patterns of sensory information could differentially recruit the same set of muscle synergies over time. These results are consistent with the fact that the same muscle synergies are also conserved across a wide range of different postural configurations in both humans (Torres-Oviedo and Ting 2010) and cats (Torres-Oviedo et al. 2006). Taken together, muscle synergies appear to be a feature of motor output organization and are not simply emergent from patterns of sensory inputs alone.

Our results support the idea that muscle synergies are used to organize the musculoskeletal system to produce a predictable biomechanical function (Chiel et al. 2009; Ting and McKay 2007), even in different postural behaviors. We previously demonstrated a consistent relationship between muscle synergy recruitment and end-point force production in cats across multiple postural configurations (Ting and Macpherson 2005; Torres-Oviedo et al. 2006). The stepping and nonstepping responses to the same support surface perturbation direction elicited different muscle activity and accelerated the body in different directions. However, our functional muscle synergy analysis revealed common relationships between patterns of muscle activity and the desired biomechanical function across both behaviors. The different individual outputs observed in nonstepping and stepping responses, such as kinematics, forces, and EMGs, arise from recruiting the same muscle synergies to accelerate the CoM in an appropriate direction to maintain balance. We observed that during human balance control the functional muscle synergies in humans were aligned with anterior-posterior and medial-lateral directions, whereas in cats, more diagonal forces were observed, possibly due to differences in the upright stance adopted by humans as opposed to the quadrupedal stance of cats (Dunbar et al. 1986). Muscle synergy recruitment in other motor behaviors has also been related to functional outputs (Ajiboye and Weir 2009; Clark et al. 2010; Krishnamoorthy et al. 2004; Weiss and Flanders 2004), suggesting that muscle synergies are organized according to function in a variety of contexts.

Because of the different mechanical dynamics of nonstepping and stepping responses, we only characterized the gross relationships between muscle activity and horizontal-plane acceleration/force direction; however, dynamic musculoskeletal simulations would be necessary to make a more quantitative assessment of the biomechanical functions of muscle synergies. Based on a prior postural response study (Jacobs and Macpherson 1996), we assumed that changes in force resulting from muscle activity could be measured at a fixed electromechanical delay of 60 ms after muscle activity. Typically, this is a reasonable assumption in the early phases of the postural response because the subject begins by standing quietly, and forces change relatively little before the muscle onset latency. In certain perturbation directions evoking stepping responses,

the perturbation caused passive loading and unloading that occurred before muscle activation changes. Therefore, we chose to exclude vertical forces from our analysis and concentrated on the relationship between muscle synergy recruitment and horizontal force generation. Furthermore, we concentrated on the force directions rather than magnitudes of the forces in stepping responses because changes in magnitude might be largely due to nonmuscular, passive dynamics of the body when falling before the step is taken. In some cases, the dynamic forces may still have masked the direction of force produced by the muscle synergy. For example, in backward perturbations, the muscle synergies did not correctly predict the CoM acceleration direction during stepping (Fig. 9, CoMy), presumably because the subject fell forward despite recruitment of a muscle synergy that would tend to accelerate the CoM backward. Although a dynamic model of stepping responses would be necessary to accurately differentiate active versus passive changes in force (Berniker et al. 2009; Kargo et al. 2010; Kautz and Hull 1993; McGowan et al. 2010; Neptune and Herzog 2000; Neptune et al. 2009), a detailed and validated human model of muscle to force interactions during standing balance control is not currently available. Nevertheless, there is a direct relationship between EMG and changes in forces and accelerations, whereas there is no direct relationship between EMG and CoM displacement and velocity, which represent the integrated effects of the applied force and the initial conditions. Therefore, while not ideal, our analysis of forces and accelerations provides evidence of directional control of the CoM that results from the recruitment of muscle synergies.

The decomposition of forces into positive and negative components was based on physiological reasons and allowed us to reveal possible muscle synergy functions. Because muscles can only produce unidirectional torques, different muscles must be activated to produce positive and negative changes in joint torques, often leading to "paradoxical" activation of multiple muscles (Valero-Cuevas 2009). In static motor tasks, the relationship between joint torque and end-point force is linear; thus, activation of any group of muscles also produces unidirectional changes in end-point force (McKay and Ting 2008). This is corroborated by previous studies in postural control demonstrating that positive and negative changes in force generation are attributed to different muscles (Jacobs and Macpherson 1996) and that different unipolar end-point force vectors are correlated to different muscle synergy activations during the initial period of the postural responses in the cat (Ting and Macpherson 2005; Torres-Oviedo et al. 2006). In our data, the positive and negative components of each force or CoM acceleration vector often had very different relationships to muscle synergy activation (Fig. 7*A*). NNMF allowed us to separately identify correlations of muscle activity to positive and negative changes in forces and accelerations. Alternative analyses, such as principal component analysis, would allow both negative and positive synergy recruitment and thus would not be adequate to reveal physiological relationships between force and muscle activity (Ting and Chvatal 2010). Our ability to correlate muscle synergy recruitment to force and acceleration was facilitated by the fact that postural responses can be considered quasistatic; background levels of muscle activity and forces are low and opposite perturbation directions recruit antagonistic sets of muscles (Jacobs and Macpherson 1996). However, as the behavior becomes more dynamic, the measured forces may include large components due to nonmuscular sources (Kautz and Hull 1993; Zajac and Gordon 1989), and it would likely be more difficult to make a clear distinction between the effects of muscle activation versus other dynamic effects on the resulting GRFs.

Despite limitations of the analysis techniques, our data indicate that the addition of stance-limb forces or CoM acceleration did not alter either the reduced dimensionality of the significant decomposition or alter the composition of the extracted muscle synergies, suggesting that there was a causal, linear relationship between muscle activity patterns and biomechanical outputs. Our analysis was also competent to reveal a component of CoM acceleration that was not attributable to muscle activity in the stance leg. For example, all subjects had one functional muscle synergy comprised only of CoM acceleration in the rightward and upward directions and no muscle activity tuned for rightward perturbations in nonstepping responses and the early portion of stepping responses (see Fig. 8). This is consistent with our previous study showing a muscle synergy tuned to rightward perturbations is only revealed during one-legged balance control but not during two-legged balance control (Torres-Oviedo and Ting 2010). Presumably, during two-legged balance control, muscle activity in the left leg (not recorded here) is responsible for producing rightward CoM acceleration in response to rightward perturbations. Furthermore, our functional muscle synergy analysis was competent to decompose the stance-limb forces into components that were attributable to muscle activity in the stance limb versus other sources.

Muscle synergies may reflect spinal and brain stem structures mediating motor control across a variety of behaviors and contexts. Neurophysiological evidence has suggested that initial postural responses in the limbs are not simply local reflexes but rather an activation of a motor pattern to achieve a biomechanical goal (Carpenter et al. 1999; Dufosse et al. 1985). Neurons in the pontomedullary reticular formation are recruited during both reactive and anticipatory postural adjustments (Schepens et al. 2008); these firings are not correlated with individual muscle activity but discharge in a manner consistent with the goal of restoring equilibrium (Stapley and Drew 2009). It is possible that there exist neural networks that specify the recruitment commands to a muscle synergy that branch with different synaptic weights to the motoneurons of the muscles in the synergy (Hart and Giszter 2010). Motoneuron synchronization has been observed in learning balance tasks (Boonstra et al. 2009), which is consistent with the fact that the recruitment, but not the structure, of muscle synergies can be modulated to explain the variation in muscle activity across postural configurations (Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2010) and walking speeds (Clark et al. 2010) as well as in hemiparetic stroke subjects (Clark et al. 2010). While such modules have been hypothesized to be encoded in the spinal cord for some tasks (Bizzi et al. 1991; Giszter et al. 1993; Hart and Giszter 2010; Saltiel et al. 2001), postural responses likely require brain stem involvement (Deliagina et al. 2008; Honeycutt et al. 2009; Macpherson et al. 1997), possibly in addition to spinal centers (Drew 2008). It remains to be seen whether the same muscle synergies are used in both reactive and voluntary postural tasks; however, similar muscle tuning curves are generated during human whole body

reaching tasks as in postural responses to perturbation (Leonard et al. 2009), suggesting that motor modules may be accessible by voluntary and reactive postural tasks in humans.

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S. A. Chvatal was primarily responsible for all data analysis and interpretation and writing the manuscript. G. Torres-Oviedo conceived of the study, designed the experimental protocol, participated in data collection, and contributed to data analysis and manuscript writing. S. A. Safavynia aided in the experimental protocol development, collected all data, and contributed to data analysis and manuscript writing. L. H. Ting supervised these activities and contributed to data analysis and writing.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

REFERENCES

Acharya S, Tenore F, Aggarwal V, Etienne-Cummings R, Schieber MH, Thakor NV. Decoding individuated finger movements using volume-constrained neuronal ensembles in the M1 hand area. *IEEE Trans Neural Syst Rehabil Eng* 16: 15–23, 2008.

Ajiboye AB, Weir RF. Muscle synergies as a predictive framework for the EMG patterns of new hand postures. *J Neural Eng* 6: 036004, 2009.

Berniker M, Jarc A, Bizzi E, Tresch MC. Simplified and effective motor control based on muscle synergies to exploit musculoskeletal dynamics. *Proc Natl Acad Sci USA* 106: 7601–7606, 2009.

Bizzi E, Mussa-Ivaldi FA, Giszter SF. Computations underlying the execution of movement: a biological perspective. *Science* 287–291, 1991.

Boonstra TW, Daffertshofer A, Roerdink M, Flipse I, Groenewoud K, Beek PJ. Bilateral motor unit synchronization of leg muscles during a simple dynamic balance task. *Eur J Neurosci* 29: 613–622, 2009.

Bosco G, Rankin AM, Poppele RE. Representation of passive hindlimb postures in cat spinocerebellar activity. *J Neurophysiol* 76: 715–726, 1996.

Burleigh AL, Horak FB, Malouin F. Modification of postural responses and step initiation: evidence for goal-directed postural interactions. *J Neurophysiol* 72: 2892–2902, 1994.

Cappellini G, Ivanenko YP, Poppele RE, Lacquaniti F. Motor patterns in human walking and running. *J Neurophysiol* 95: 3426–3437, 2006.

Carpenter MG, Allum JH, Honegger F. Directional sensitivity of stretch reflexes and balance corrections for normal subjects in the roll and pitch planes. *Exp Brain Res* 129: 93–113, 1999.

Cheung VC, d'Avella A, Bizzi E. Adjustments of motor pattern for load compensation via modulated activations of muscle synergies during natural behaviors. *J Neurophysiol* 101: 1235–1257, 2009a.

Cheung VC, d'Avella A, Tresch MC, Bizzi E. Central and sensory contributions to the activation and organization of muscle synergies during natural motor behaviors. *J Neurosci* 25: 6419–6434, 2005.

Cheung VC, Piron L, Agostini M, Silvoni S, Turolla A, Bizzi E. Stability of muscle synergies for voluntary actions after cortical stroke in humans. *Proc Natl Acad Sci USA* 106: 19563–19568, 2009b.

Chiel HJ, Ting LH, Ekeberg O, Hartmann MJ. The brain in its body: motor control and sensing in a biomechanical context. *J Neurosci* 29: 12807–12814, 2009.

Clark DJ, Ting LH, Zajac FE, Neptune RR, Kautz SA. Merging of healthy motor modules predicts reduced locomotor performance and muscle coordination complexity post-stroke. *J Neurophysiol* 103: 844–857, 2010.

d'Avella A, Bizzi E. Shared and specific muscle synergies in natural motor behaviors. *Proc Natl Acad Sci USA* 102: 3076–3081, 2005.

d'Avella A, Portone A, Fernandez L, Lacquaniti F. Control of fast-reaching movements by muscle synergy combinations. *J Neurosci* 26: 7791–7810, 2006.

d'Avella A, Saltiel P, Bizzi E. Combinations of muscle synergies in the construction of a natural motor behavior. *Nat Neurosci* 6: 300–308, 2003.

Danna-Dos-Santos A, Slomka K, Zatsiorsky VM, Latash ML. Muscle modes and synergies during voluntary body sway. *Exp Brain Res* 179: 533–550, 2007.

Deliagina TG, Beloozerova IN, Zelenin PV, Orlovsky GN. Spinal and supraspinal postural networks. *Brain Res Rev* 57: 212–221, 2008.

Drew T, Kalaska J, Krouchev N. Muscle synergies during locomotion in the cat: a model for motor cortex control. *J Physiol* 586: 1239–1245, 2008.

Dufosse M, Hugon M, Massion J. Postural forearm changes induced by predictable in time or voluntary triggered unloading in man. *Exp Brain Res* 60: 330–334, 1985.

Dunbar DC, Horak FB, Macpherson JM, Rushmer DS. Neural control of quadrupedal and bipedal stance: implications for the evolution of erect posture. *Am J Phys Anthropol* 69: 93–105, 1986.

Efron B. *An Introduction to the Bootstrap*. New York: Chapman & Hall, 1993.

Flash T, Hochner B. Motor primitives in vertebrates and invertebrates. *Curr Opin Neurobiol* 15: 660–666, 2005.

Giszter S, Patil V, Hart C. Primitives, premotor drives, and pattern generation: a combined computational and neuroethological perspective. *Prog Brain Res* 165: 323–346, 2007.

Giszter SF, Mussa-Ivaldi FA, Bizzi E. Convergent force fields organized in the frog's spinal cord. *J Neurosci* 13: 467–491, 1993.

Gollhofer A, Horstmann GA, Berger W, Dietz V. Compensation of translational and rotational perturbations in human posture: stabilization of the centre of gravity. *Neurosci Lett* 105: 73–78, 1989.

Hamed SB, Schieber MH, Pouget A. Decoding M1 neurons during multiple finger movements. *J Neurophysiol* 98: 327–333, 2007.

Hart CB, Giszter SF. A neural basis for motor primitives in the spinal cord. *J Neurosci* 30: 1322–1336, 2010.

Hart CB, Giszter SF. Modular premotor drives and unit bursts as primitives for frog motor behaviors. *J Neurosci* 24: 5269–5282, 2004.

Honeycutt CF, Gottschall JS, Nichols TR. Electromyographic responses from the hindlimb muscles of the decerebrate cat to horizontal support surface perturbations. *J Neurophysiol* 101: 2751–2761, 2009.

Horak FB, Macpherson JM. Postural orientation and equilibrium. In: *Handbook of Physiology. Exercise: Regulation and Integration of Multiple Systems*. Bethesda, MD: Am. Physiol. Soc., 1996, sect. 12, chapt. 7, p. 255–292.

Horak FB, Nashner LM. Central programming of postural movements: adaptation to altered support-surface configurations. *J Neurophysiol* 55: 1369–1381, 1986.

Inglis JT, Horak FB, Shupert CL, Jones-Rycewicz C. The importance of somatosensory information in triggering and scaling automatic postural responses in humans. *Exp Brain Res* 101: 159–164, 1994.

Ivanenko YP, Cappellini G, Dominici N, Poppele RE, Lacquaniti F. Coordination of locomotion with voluntary movements in humans. *J Neurosci* 25: 7238–7253, 2005.

Ivanenko YP, Grasso R, Zago M, Molinari M, Scivoletto G, Castellano V, Macellari V, Lacquaniti F. Temporal components of the motor patterns expressed by the human spinal cord reflect foot kinematics. *J Neurophysiol* 90: 3555–3565, 2003.

Ivanenko YP, Wright WG, Gurfinkel VS, Horak F, Cordo P. Interaction of involuntary post-contraction activity with locomotor movements. *Exp Brain Res* 169: 255–260, 2006.

Jacobs R, Macpherson JM. Two functional muscle groupings during postural equilibrium tasks in standing cats. *J Neurophysiol* 76: 2402–2411, 1996.

Kargo WJ, Giszter SF. Rapid correction of aimed movements by summation of force-field primitives. *J Neurosci* 20: 409–426, 2000.

Kargo WJ, Ramakrishnan A, Hart CB, Rome LC, Giszter SF. A simple experimentally based model using proprioceptive regulation of motor primitives captures adjusted trajectory formation in spinal frogs. *J Neurophysiol* 103: 573–590, 2010.

Kautz SA, Hull ML. A theoretical basis for interpreting the force applied to the pedal in cycling. *J Biomech* 26: 155–165, 1993.

King LA, Horak FB. Lateral stepping for postural correction in Parkinson's disease. *Arch Phys Med Rehabil* 89: 492–499, 2008.

Krishnamoorthy V, Latash ML, Scholz JP, Zatsiorsky VM. Muscle modes during shifts of the center of pressure by standing persons: effect of instability and additional support. *Exp Brain Res* 157: 18–31, 2004.

Latash ML, Krishnamoorthy V, Scholz JP, Zatsiorsky VM. Postural synergies and their development. *Neural Plast* 12: 119–130 and 172–263, 2005.

Lee DD, Seung HS. Learning the parts of objects by non-negative matrix factorization. *Nature* 401: 788–791, 1999.

Leonard JA, Brown RH, Stapley PJ. Reaching to multiple targets when standing: the spatial organization of feedforward postural adjustments. *J Neurophysiol* 101: 2120–2133, 2009.

Macpherson JM, Fung J, Jacobs R. Postural orientation, equilibrium, and the spinal cord. *Adv Neurol* 72: 227–232, 1997.

Maki BE, McIlroy WE. The role of limb movements in maintaining upright stance: the "change-in-support" strategy. *Phys Ther* 77: 488–507, 1997.

Massion J. Movement, posture and equilibrium: interaction and coordination. *Prog Neurobiol* 38: 35–56, 1992.

McGowan CP, Neptune RR, Herzog W. A phenomenological model and validation of shortening-induced force depression during muscle contractions. *J Biomech* 43: 449–454, 2010.

McIlroy WE, Maki BE. Changes in early "automatic" postural responses associated with the prior-planning and execution of a compensatory step. *Brain Res* 631: 203–211, 1993a.

McIlroy WE, Maki BE. Task constraints on foot movement and the incidence of compensatory stepping following perturbation of upright stance. *Brain Res* 616: 30–38, 1993b.

McKay JL, Ting LH. Functional muscle synergies constrain force production during postural tasks. *J Biomech* 41: 299–306, 2008.

Muceli S, Boye AT, d'Avella A, Farina D. Identifying representative synergy matrices for describing muscular activation patterns during multidirectional reaching in the horizontal plane. *J Neurophysiol* 103: 1532–1542, 2010.

Nashner LM. Fixed patterns of rapid postural responses among leg muscles during stance. *Exp Brain Res* 30: 13–24, 1977.

Nashner LM, Mccollum G. The organization of human postural movements–a formal basis and experimental synthesis. *Behav Brain Sci* 8: 135–150, 1985.

Neptune RR, Herzog W. Adaptation of muscle coordination to altered task mechanics during steady-state cycling. *J Biomech* 33: 165–172, 2000.

Neptune RR, McGowan CP, Kautz SA. Forward dynamics simulations provide insight into muscle mechanical work during human locomotion. *Exerc Sport Sci Rev* 37: 203–210, 2009.

Overduin SA, d'Avella A, Roh J, Bizzi E. Modulation of muscle synergy recruitment in primate grasping. *J Neurosci* 28: 880–892, 2008.

Perry SD, McIlroy WE, Maki BE. The role of plantar cutaneous mechanoreceptors in the control of compensatory stepping reactions evoked by unpredictable, multi-directional perturbation. *Brain Res* 877: 401–406, 2000.

Raasch CC, Zajac FE. Locomotor strategy for pedaling: muscle groups and biomechanical functions. *J Neurophysiol* 82: 515–525, 1999.

Robert T, Zatsiorsky VM, Latash ML. Multi-muscle synergies in an unusual postural task: quick shear force production. *Exp Brain Res* 2008.

Runge CF, Shupert CL, Horak FB, Zajac FE. Role of vestibular information in initiation of rapid postural responses. *Exp Brain Res* 122: 403–412, 1998.

Saltiel P, Wyler-Duda K, D'Avella A, Tresch MC, Bizzi E. Muscle synergies encoded within the spinal cord: evidence from focal intraspinal NMDA iontophoresis in the frog. *J Neurophysiol* 85: 605–619, 2001.

Schepens B, Stapley P, Drew T. Neurons in the pontomedullary reticular formation signal posture and movement both as an integrated behavior and independently. *J Neurophysiol* 100: 2235–2253, 2008.

Scholz JP, Schoner G, Hsu WL, Jeka JJ, Horak F, Martin V. Motor equivalent control of the center of mass in response to support surface perturbations. *Exp Brain Res* 180: 163–179, 2007.

Stapley PJ, Drew T. The pontomedullary reticular formation contributes to the compensatory postural responses observed following removal of the support surface in the standing cat. *J Neurophysiol* 101: 1334–1350, 2009.

Stapley PJ, Ting LH, Hulliger M, Macpherson JM. Automatic postural responses are delayed by pyridoxine-induced somatosensory loss. *J Neurosci* 22: 5803–5807, 2002.

Ting LH. Dimensional reduction in sensorimotor systems: a framework for understanding muscle coordination of posture. *Prog Brain Res* 165: 299–321, 2007.

Ting LH, Chvatal SA. Decomposing muscle activity in motor tasks: methods and interpretation. In: *Motor Control: Theories, Experiments, and Applications*, edited by Danion F, Latash ML. Oxford: Oxford Univ. Press, 2010, p. 102–138.

Ting LH, Kautz SA, Brown DA, Zajac FE. Phase reversal of biomechanical functions and muscle activity in backward pedaling. *J Neurophysiol* 81: 544–551, 1999.

Ting LH, Macpherson JM. A limited set of muscle synergies for force control during a postural task. *J Neurophysiol* 93: 609–613, 2005.

Ting LH, Macpherson JM. Ratio of shear to load ground-reaction force may underlie the directional tuning of the automatic postural response to rotation and translation. *J Neurophysiol* 92: 808–823, 2004.

Ting LH, McKay JL. Neuromechanics of muscle synergies for posture and movement. *Curr Opin Neurobiol* 17: 622–628, 2007.

Ting LH, van Antwerp KW, Scrivens JE, McKay JL, Welch TD, Bingham JT, DeWeerth SP. Neuromechanical tuning of nonlinear postural control dynamics. *Chaos* 19: 026111, 2009.

Torres-Oviedo G, Macpherson JM, Ting LH. Muscle synergy organization is robust across a variety of postural perturbations. *J Neurophysiol* 96: 1530–1546, 2006.

Torres-Oviedo G, Ting LH. Muscle synergies characterizing human postural responses. *J Neurophysiol* 98: 2144–2156, 2007.

Torres-Oviedo G, Ting LH. Subject-specific muscle synergies in human balance control are consistent across different biomechanical contexts. *J Neurophysiol* 2010.

Tresch MC, Cheung VC, d'Avella A. Matrix factorization algorithms for the identification of muscle synergies: evaluation on simulated and experimental data sets. *J Neurophysiol* 95: 2199–2212, 2006.

Tresch MC, Saltiel P, Bizzi E. The construction of movement by the spinal cord. *Nat Neurosci* 2: 162–167, 1999.

Trivedi H, Leonard JA, Ting LH, Stapley PJ. Postural responses to unexpected perturbations of balance during reaching. *Exp Brain Res* 202: 485–491, 2010.

Valero-Cuevas FJ. A mathematical approach to the mechanical capabilities of limbs and fingers. *Adv Exp Med Biol* 629: 619–633, 2009.

van der Linden MH, Marigold DS, Gabreels FJ, Duysens J. Muscle reflexes and synergies triggered by an unexpected support surface height during walking. *J Neurophysiol* 97: 3639–3650, 2007.

Weber DJ, Stein RB, Everaert DG, Prochazka A. Limb-state feedback from ensembles of simultaneously recorded dorsal root ganglion neurons. *J Neural Eng* 4: S168–180, 2007.

Weiss EJ, Flanders M. Muscular and postural synergies of the human hand. *J Neurophysiol* 92: 523–535, 2004.

Welch TD, Ting LH. A feedback model reproduces muscle activity during human postural responses to support-surface translations. *J Neurophysiol* 99: 1032–1038, 2008.

Winter DA. *Biomechanics and Motor Control of Human Movement*. New York: Wiley, 1990.

Woollacott M, Shumway-Cook A. Attention and the control of posture and gait: a review of an emerging area of research. *Gait Posture* 16: 1–14, 2002.

Yakovenko S, Krouchev NI, Drew T. Sequential activation of motor cortical neurons contributes to intralimb coordination during reaching in the cat by modulating muscle synergies. *J Neurophysiol* 105: 388–409, 2010.

Zajac FE, Gordon ME. Determining muscle's force and action in multi-articular movement. *Exerc Sport Sci Rev* 17: 187–230, 1989.

Zar J. Biostatistical Analysis. Upper Saddle River, NJ: Prentice-Hall, 1999.

Zettel JL, McIlroy WE, Maki BE. Can stabilizing features of rapid triggered stepping reactions be modulated to meet environmental constraints? *Exp Brain Res* 145: 297–308, 2002.