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Subject-Specific Muscle Synergies in Human Balance Control Are Consistent Across Different Biomechanical Contexts

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Torres-Oviedo G, Ting LH. Subject-specific muscle synergies in human balance control are consistent across different biomechanical contexts. *J Neurophysiol* 103: 3084–3098, 2010. First published April 14, 2010; doi:10.1152/jn.00960.2009. The musculoskeletal redundancy of the body provides multiple solutions for performing motor tasks. We have proposed that the nervous system solves this unconstrained problem through the recruitment of motor modules or functional muscle synergies that map motor intention to action. Consistent with this hypothesis, we showed that trial-by-trial variations in muscle activation for multidirectional balance control in humans were constrained by a small set of muscle synergies. However, apparent muscle synergy structures could arise from characteristic patterns of sensory input resulting from perturbations or from low-dimensional optimal motor solutions. Here we studied electromyographic (EMG) responses for balance control across a range of biomechanical contexts, which alter not only the sensory inflow generated by postural perturbations, but also the muscle activation patterns used to restore balance. Support-surface translations in 12 directions were delivered to subjects standing in six different postural configurations: one-leg, narrow, wide, very wide, crouched, and normal stance. Muscle synergies were extracted from each condition using nonnegative matrix factorization. In addition, muscle synergies from the normal stance condition were used to reconstruct muscle activation patterns across all stance conditions. A consistent set of muscle synergies were recruited by each subject across conditions. When balance demands were extremely different from the normal stance (e.g., one-legged or crouched stance), task-specific muscle synergies were recruited in addition to the preexisting ones, rather generating de novo muscle synergies. Taken together, our results suggest that muscle synergies represent consistent motor modules that map intention to action, regardless of the biomechanical context of the task.

INTRODUCTION

The control of balance requires sensorimotor transformations that allow the nervous system to rapidly interpret multiple sensory input signals from all segments of the body to produce context-dependent muscle activation patterns that stabilize the body. In humans, we previously observed that the variations in muscle activation patterns evoked in response to different directions of support-surface movements in the horizontal plane could be described by a limited set of muscle synergies (Torres-Oviedo and Ting 2007). We define muscle synergies as invariant patterns of activation across multiple muscles that are combined to produce complex muscle activation patterns. We hypothesize that variations in muscle activity for movement are generated through the flexible recruitment of a limited set of muscle synergies (for review see Ting and McKay 2007; Tresch and Jarc 2009). To challenge our hypothesis, we investigated whether muscle synergy structures are consistent across conditions in which the biomechanical and sensory context of the postural task change and where large variations in muscle activity are observed. To this end we examined muscle activation patterns in postural responses to perturbations administered to subjects standing in six different postural configurations.

Consistency in muscle synergy structure and function across different biomechanical contexts would suggest that muscle synergies represent motor modules that map motor intention to action. Accordingly, changes in muscle activity would be due to the modulation of neural commands that recruit muscle synergies, but not to changes in the structure of the muscle synergies themselves. Studies in frogs demonstrate that common muscle synergy structures produce similar functions like extending the leg across behaviors with different biomechanical contexts such as swimming, jumping, and wiping (d'Avella and Bizzi 2005). Similarly, in cat postural responses, we demonstrated that changes in mean muscle activity across different postural configurations could be explained by modulating the recruitment of the same set of muscle synergies (Torres-Oviedo et al. 2006). These muscle synergies appear to produce the same endpoint force vector relative to the limb across a range of postural configurations (McKay and Ting 2008; Torres-Oviedo et al. 2006). In human pedaling and walking, consistent functional roles of muscle synergies have been demonstrated to allow robust behaviors across locomotor speeds (Clark et al. 2010; McGowan et al. 2010; Neptune et al. 2009; Raasch and Zajac 1999). In human balance control, we demonstrated that trial-by-trial changes in electromyographic (EMG) patterns across multiple muscles could be accounted for by the recruitment of a consistent set of muscle synergies to restore balance (Torres-Oviedo and Ting 2007). However, in our prior human study we examined subjects standing only in their preferred postural configuration. Therefore it is unknown whether the identified muscle synergies were consistent because they reflected motor modules for mapping intention to action or because they simply reflected the consistent biomechanical context of the balance task that we studied.

Although, the consistency of muscle synergies in response to perturbations could be due to the shaping of motor outputs by characteristic patterns of somatosensory inflow, evidence suggests that this is not the case. During postural perturbations to standing balance, somatosensory information arising from the joints and skin is critical to the timing of the initial burst of postural muscle activity (Inglis et al. 1994; Stapley et al. 2002). Moreover, the specific pattern of sensory input is determined by the interactions between the perturbation and the musculo-

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skeletal configuration of the limb (Honeycutt et al. 2009). Patterns of sensory input are therefore expected to change with postural configuration. If muscle synergy structures are shaped by somatosensory patterns, then their structure would be predicted to change in direct relation to sensory input patterns. However, a decoupling of somatosensory patterns and motor output patterns has been demonstrated in both human and cat postural responses, whereby perturbations causing *opposite* joint motions and loadings give rise to similar muscle activation patterns (Nashner 1977; Ting and Macpherson 2004). This demonstrates that postural muscle activity is not consistently related to specific patterns of sensory inputs. In contrast, the same muscle activation patterns across different perturbation paradigms are predicted by the required direction of center of mass (CoM) motion for balance control, suggesting that the motor output is related to the performance of a task level goal (Gollhofer et al. 1989; Ting and Macpherson 2004). Moreover, in cat postural control we demonstrated that the same muscle synergies could account for EMG responses to perturbations that induced opposite changes in joint angle (i.e., different sensory inflow), but similar (CoM) displacements (Torres-Oviedo et al. 2006). Similarly, muscle synergy structure is largely preserved after deafferentation, in which changes in motor output patterns are attributable to changes in the recruitment of muscle synergies (Cheung et al. 2005; Kargo et al. 2010). These results further support the idea that muscle synergies are motor output modules whose recruitment, but not structure, is altered by changing patterns of sensory inflow. An implication is that changes in patterns of local somatosensory feedback associated with different postural configurations would not be expected to alter muscle synergy structure.

It has also been suggested that the identification of muscle synergies in motor tasks reflects the optimal muscle coordination pattern to control the limb in a given configuration, rather than modularity of motor outputs (Fagg et al. 2002; Kurtzer et al. 2006). The invariant muscle synergies that we identified in postural control could be emergent patterns based on optimal control of the musculoskeletal system and not explicitly encoded in the nervous system. An implication is that the optimal muscle activation pattern would be expected to change when the biomechanical context of the task is altered. However, there has been surprising robustness in the identification of muscle synergies across different motor tasks, such as swimming and locomotion in frogs (Cheung et al. 2005; d'Avella and Bizzi 2005), different postural configurations in cats (Torres-Oviedo et al. 2006), or when grasping different shaped objects (Overduin et al. 2008). Musculoskeletal modeling studies have also demonstrated that although muscle synergy structures could be optimized for a particular biomechanical task or objective function, they may be more generally applied to produce a wider repertoire of related tasks (Berniker et al. 2009; Raasch and Zajac 1999; Valero-Cuevas et al. 1998) In cat postural control, we demonstrated that postural forces were predicted to rotate, as in experimental observations, only if muscle synergy constraints were imposed, but not if individual muscle coordination was allowed (McKay and Ting 2008). Thus although muscle synergies might indeed be shaped by optimality principles, they might still be encoded within the nervous system as a heuristic representation of a particular optimal motor solution. If the identified muscle synergies are emergent from optimization processes, then we would predict muscle synergy structures to change as the biomechanical context of muscle actions varies across different postural configurations. Alternately, if muscle synergies reflect a set of motor modules that are generally recruited to perform particular motor tasks, then we would predict them to be invariant across different postural configurations.

Here we altered the postural configuration of subjects to test the consistency of muscle synergies across different biomechanical and sensory contexts. Moderate changes in postural configuration consisted of changes in stance width and have been shown to alter the magnitude of EMG responses (Henry et al. 2001). Extreme changes in postural configuration consisted of standing in a crouched configuration or on one leg, which have been shown to alter amplitude, latency (crouch; Burtner et al. 1998), and directional tuning (one-leg; Tropp and Odenrick 1988) of EMG responses. We observed that the structure of muscle synergies previously identified (Torres-Oviedo and Ting 2007) was independent of the musculoskeletal configuration. The large variations in EMG activity within and across biomechanical contexts were accounted for by the recruitment of consistent sets of subject-specific muscle synergies. Also, when balance demands were extremely different from the typical stance (e.g., one-legged or crouched stance), task-specific muscle synergies were recruited in addition to the preexisting ones, rather generating de novo muscle synergies. In sum, these results suggest that muscle synergies simplify balance control by providing consistent motor outputs that map intention to action, regardless of the biomechanical context of the postural task.

METHODS

Experimental setup

To test the degree to which the biomechanical context of the postural task influenced the structure and recruitment of muscle synergies used for balance control, we studied human responses to balance perturbations in multiple stance configurations. Subjects stood in six postural configurations and experienced unexpected support-surface translations in 12 evenly distributed directions in the horizontal plane (Fig. 1), yielding a total of 72 different combinations of perturbation direction and postural configuration tested in each subject. Data were collected over 2 consecutive days. In each session, both postural configuration and perturbation direction were randomized. In all, nine healthy subjects (five females and four males; mean age: 21.9 $\pm$ 3.6 yr; mean height: 67.4 $\pm$ 2.9 in.; mean weight: 140.4 $\pm$ 17.8 lb; mean body mass index [BMI]: 21.6 $\pm$ 1.7) participated in the study. All experimental protocols were approved by the Georgia Tech and Emory University Institutional Review Boards.

To induce a large degree of variability, EMG responses were evoked during both "moderate" and "extreme" variations in postural configuration. Additional variability in EMG responses was further introduced within trials of the same stance conditions because we did not explicitly monitor or prescribe the joint angles or center of pressure location prior to each trial. For "moderate" variations in postural configuration subjects were instructed to stand at either *narrow*, *normal*, or *wide* stance widths by placing their heels on marks located 9, 19, and 30 cm apart, respectively. These conditions were previously shown to alter the magnitude of EMG responses in humans (Henry et al. 1998, 2001). For "extreme" variations in postural configuration subjects were instructed to stand at the *widest* stance width, in *one-leg* stance, and in a *crouched* stance. The distance between the feet in the widest stance

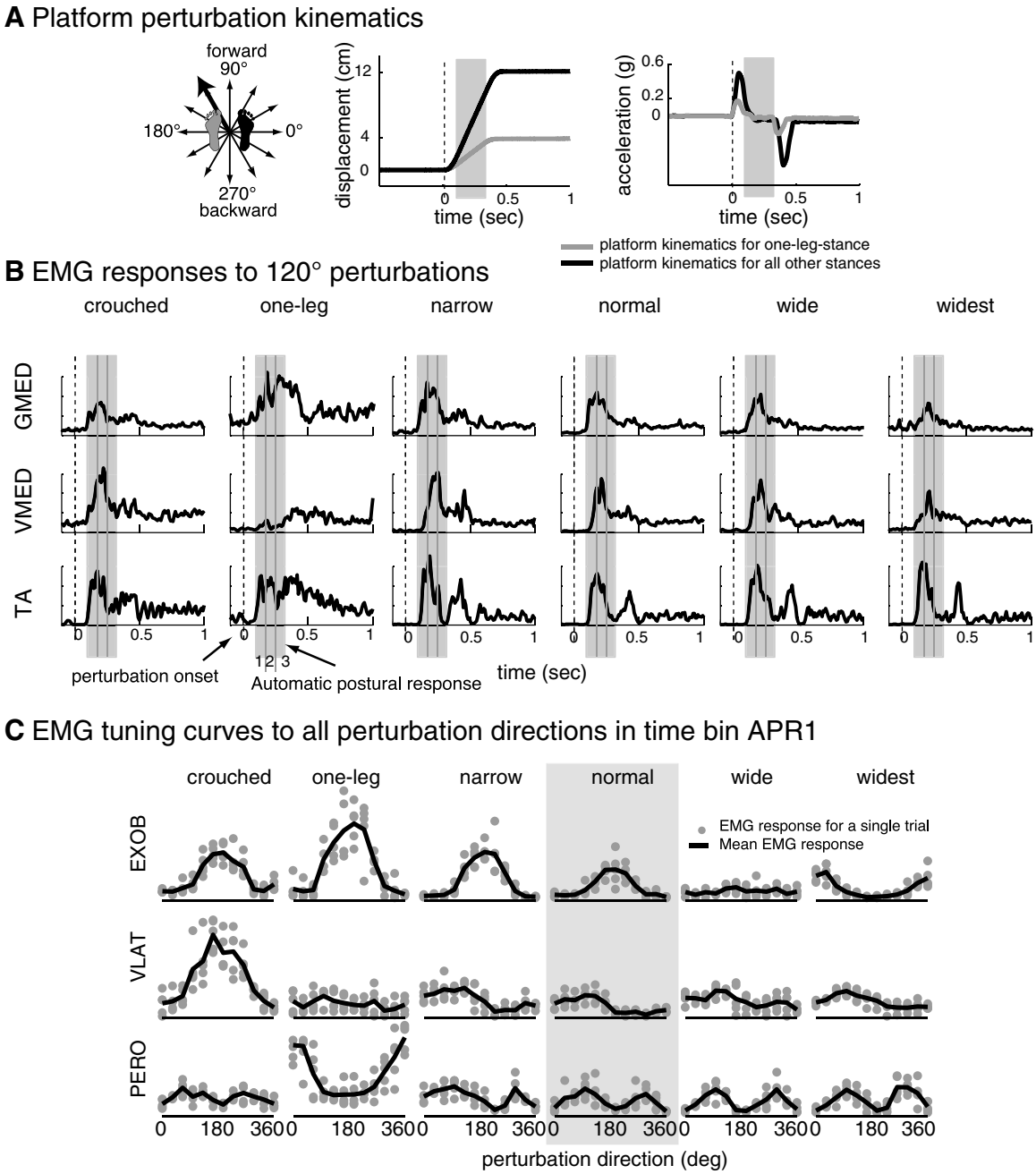

FIG. 1. Example of changes in muscle activity patterns across postural configurations during electromyographic (EMG) responses to a leftward-forward perturbation of the support surface. *A*: perturbations were induced by a ramp-and-hold motion of the support surface. The same parameters of platform motion were used for perturbations in all stance conditions except for the one-leg stance, in which a smaller platform motion was used. *B*: example EMG activity of tibialis anterior (TA), vastus medialis (VMED), and gluteus medius (GMED) in response to the same perturbation direction under different postural configurations. Changes in muscle activity typically occur 100 ms following the onset of platform motion (vertical dashed line). Mean EMG activity in 3 time bins of 75 ms (shaded areas; EMG_{APR1}, EMG_{APR2}, EMG_{APR3}) were used in the analysis. *C*: representative tuning curves of external oblique (EXOB), vastus lateralis (VLAT), and peroneus (PERO) during EMG_{APR1} of a sample subject standing in all stance conditions. Directions of peak muscle activity were conserved in the normal, narrow, and wide configurations, but could change in the one-leg, crouched, and widest stance conditions. Black traces indicate the mean response and gray dots represent responses in each trial. Intertrial variations in EMG responses were also observed in all stance conditions, as shown by the spread in gray dots indicating response level during a single trial.

was 60 cm, twice that of the wide stance. In the one-leg stance, subjects were instructed to maintain their balance on their right leg (dominant leg for all subjects) throughout the entire platform motion, without allowing the ankle of the nonstance leg to be braced against the stance limb. In the crouched stance, subjects bent their knees (~20° knee flexion) while maintaining their feet in contact with the floor and their torso relatively upright.

On the first day, normal, narrow, wide, and widest stances were tested; normal, one-leg, and crouched stances were tested on the second day. The normal stance was collected on each day to act as a control for comparisons across days. In each session, five replicates of each condition were collected. Thus a total of ten replicates were collected for normal stance; these data have been previously analyzed and published (Torres-Oviedo and Ting 2007). Ramp-and-hold sup-

port-surface translations of 12.4 cm total displacement, 35 cm/s peak velocity, and 0.5 g (~490 cm/s^2) peak acceleration were used for all experimental conditions except for the one-leg stance, for which a smaller perturbation of 4 cm total displacement, 12 cm/s peak velocity, and 0.2 g (~196 cm/s^2) peak acceleration were used (Fig. 1*A*).

EMG activity was recorded from 16 leg and lower-back muscles of the subject's right side. Electrode positions on the subject's body were marked to ensure similar electrode placement in both experimental sessions. The following muscles were recorded: rectus abdominalis (REAB), tensor fascia lata (TFL), biceps femoris long head (BFLH), tibialis anterior (TA), semitendinosus (SEMT), semimembranosus (SEMB), rectus femoris (RFEM), peroneus (PERO), medial gastrocnemius (MGAS), lateral gastrocnemius (LGAS), erector spinae (ERSP), external oblique (EXOB), gluteus medius (GMED), vastus lateralis (VLAT), vastus medialis (VMED), and soleus (SOL). Raw EMG data were filtered and processed off-line using a set of custom MATLAB routines. The entire time course of the raw EMG data was high-pass filtered at 35 Hz, demeaned, rectified, and low-pass filtered at 40 Hz. EMGs were normalized to their maximum mean values measured across perturbation directions in the normal stance configuration. Normalizing the data in this way reduced sensitivity to outliers.

Data processing

Postural response activity for each trial was characterized by the mean EMG activity in each of four time bins: a 280-ms background period (BK) that ended 170 ms before the perturbation and each of three 75-ms time bins beginning 100 ms (automatic postural response 1 [APR_1]), 175 ms (APR_2), and 250 ms (APR_3) after perturbation onset (Fig. 1*B*). These time bins can characterize the basic temporal phases of EMG responses of individual muscles (Diener et al. 1988; Torres-Oviedo and Ting 2007). Data from each of the 16 muscles in each postural configuration consisted of a vector of data composed of 4 time bins × 12 directions × 5 trials = 240 data points (480 for normal stance). Therefore across all six postural configurations we analyzed 26,880 data points.

To ensure the activity in all muscles was equally weighted in the muscle synergy extraction algorithms, muscle data vectors consisting of EMG_{BK}, EMG_{APR1}, EMG_{APR2}, and EMG_{APR3} across all perturbation directions from the normal stance condition were further normalized to have unit variance before muscle synergy extraction. Then, muscle data vectors from all the other stance conditions were normalized with the same normalization factors to maintain consistent units across conditions.

Data analysis

In all subjects, muscle synergies were extracted for each stance condition using a nonnegative matrix factorization algorithm described in detail in the following text. We determined the number of muscle synergies that best described each data set by choosing the smallest number of muscle synergies that could account for 75% of the variability of that data set using the same local and global criteria from our previous studies (Torres-Oviedo and Ting 2007; Torres-Oviedo et al. 2006). Previously we demonstrated that muscle synergies from normal stance were not significantly different when extracted from data collected on 2 consecutive days (Torres-Oviedo and Ting 2007). Because these results demonstrate that the differences in electrode placement did not affect muscle synergy recruitment, we were able to compare muscle synergies across all conditions.

To overcome the known difficulties when comparing muscle synergies across data sets, we also used an alternate approach of identifying shared and specific muscle synergies across conditions as in previous studies (Cheung et al. 2005, 2009a; Torres-Oviedo et al. 2006). We examined whether muscle synergies from normal stance trials—the control condition—in each subject could account for muscle activation patterns in all of the other postural configurations (test conditions). Task-specific muscle synergies were subsequently extracted when control muscle synergies could not account for important features in the test conditions. This approach was necessary because *1*) muscle synergies cannot be reliably identified in data sets where they are not recruited (Torres-Oviedo et al. 2006) and *2*) muscle synergies that are recruited independently in one condition but covary in another condition will appear merged and cause an apparent reduction in the number of muscle synergies (Cheung et al. 2005; Clark et al. 2010; Raasch and Zajac 1999; Saltiel et al. 2001; Ting et al. 1999). We then compared the extracted muscle synergies for each stance to the control and task-specific muscle synergies. Finally to further cross-validate our results, we also compared them to muscle synergies extracted from the entire data pool.

Extraction of muscle synergies from a single postural configuration

Muscle synergies were extracted using nonnegative matrix factorization, a linear decomposition technique previously presented (Cheung et al. 2005; Lee and Seung 2001; Torres-Oviedo and Ting 2007; Torres-Oviedo et al. 2006; Tresch et al. 2006). This linear decomposition technique assumes that each muscle activation pattern M, evoked by a perturbation at a given time period and stance configuration (e.g., Fig. 8*B*; Trial 1 in one-leg condition) is composed of a linear combination of a few (N_{syn}) muscle synergies W, each recruited by synergy scaling coefficient c_i. Thus the predicted muscle activation pattern $\hat{M}$ takes the form

$$\hat{M}(t) = \sum_{i=1}^{i=N_{syn}} c_i(t) W_i \qquad c_i \geq 0 \quad W_i \geq 0 \tag{1}$$

The ith muscle synergy W_i is represented as a vector that specifies a spatial pattern of muscle activity identified in the control condition data set. Each element of W_i represents a muscle whose relative contribution to the muscle synergy is time invariant and takes a value between 0 and 1. The nonnegative scaling coefficient c_i describes the recruitment of the muscle synergy, representing the purported neural command to the muscle synergy that determines the relative contribution of W_i to the overall predicted muscle activation pattern $\hat{M}$. The set of c_i values scaling W_i across all perturbation directions during quiet stance and during the three automatic postural response (APR) periods is the vector C_i. The components of C_i are tuning curves that describe how the recruitment of W_i changes as a function of perturbation direction and time.

In all our subjects we extracted muscle synergies from the control condition using an iterative process where N_{syn} varied between 1 and 16, the number of muscles. Then using the control muscle synergies we determined the coefficients that would best reconstruct the EMG responses at each test condition: C_{wide}, C_{widest}, $C_{crouched}$, $C_{one\text{-}legged}$, and C_{narrow}, or C_{normal}. We selected the smallest number of muscle synergies that could adequately reconstruct background and APR responses of each muscle in all the trials of control and test conditions. This was determined by both global and local criteria, which ensured that muscle synergies represented actual features in the data set and not of the noise. We used variability accounted for (VAF), defined as 100 × uncentered Pearson correlation coefficient (Torres-Oviedo et al. 2006; Zar 1999), to quantify the goodness of the data reconstruction by the muscle synergies. First, we plotted the overall VAF, indicating the goodness of the fit of the overall data, against the number of muscle synergies and looked for the inflection point beyond which additional increase in muscle synergies caused only small increments in VAF. Next, we used a local criterion to add muscle synergies whose recruitment accounted for a relatively smaller percentage of the overall VAF but provided significant improvement (>75% VAF) in the reconstruction of a particular direction, condition,

or muscle activity pattern. These criteria ensured that each muscle tuning curve at all stance configurations would be well reconstructed, so that the critical spatiotemporal features of each muscle activation pattern were well accounted for by the muscle synergies. In general, by satisfying our local criteria, the total VAF in the data set was well over 90%. If the addition of a muscle synergy contributed evenly to the VAF of directions, conditions, or muscles, it was not included because it was considered to represent only random variations in the data and not those due to either direction or condition.

Extraction of task-specific muscle synergies

Task-specific muscle synergies W^{test} were extracted in test conditions where control muscle synergies extracted from the normal stance (control condition) were not adequate to account for >75% of the variability in muscle activation patterns. Task-specific muscle synergies were relevant only to the test conditions and they were identified by applying the same principles used in the reformulation of the NMF algorithm by Cheung et al. (2005, 2009a). We provided the algorithm with the test condition data and the control muscle synergies W. The algorithm first performs a least-squares fit to determine the nonnegative coefficients C_{test} that would best reconstruct the test condition data using W. Subsequently, the algorithm determines W^{test} to reconstruct the test condition data not accounted for by W. Thus similar to a multiple regression, the net muscle activation pattern in the test condition $\hat{M}^{test}$ was obtained by the projection of the test data onto W and W^{test} extracted from the residual data. Stated formally

$$\hat{M}^{test}(t) = \sum_{i=1}^{i=N_{syn}} c_{test\,i}(t) W_i + \sum_{i=1}^{i=N\,test} c_i^{test}(t) W_i^{test}$$
$$c_{test\,i},\, c_i^{test} \geq 0 \quad W_i,\, W_i^{test} \geq 0 \tag{2}$$

The ith task-specific muscle synergy W_i^{test} is a time-invariant nonnegative vector that specifies a spatial pattern of muscle activity featured in the test data only. The magnitude of its contribution to $\hat{M}^{test}$ is determined by c_i^{test}, representing the neural command to W_i^{test}. C_i^{test} is the set of c_i^{test} values scaling W_i^{test} across all perturbation directions and time periods. Thus C^{test} describes how the recruitment of task-specific muscle synergies W^{test} change as a function of perturbation direction and time.

Validation of subject-specific and task-specific muscle synergies

To validate the number and pattern of muscle synergies per subject, we extracted muscle synergies independently from different portions of the data set. Muscle synergies were extracted not only from each stance condition but also from data pooled across all stance conditions. For each subject, we calculated correlation coefficients to compare control and task-specific muscle synergies to those extracted from different portions of the entire data set (i.e., from each stance condition or all stance conditions).

In addition, to test whether intertrial variability had a structure specific to each subject, we compared the ability to reproduce each subject's EMG patterns in all stance conditions by synergies from each subject's own data versus those from the other subjects. One-way ANOVA on the variability accounted for per muscle synergy set was performed. The type of muscle synergies used was set as a factor with Fisher's least significant difference (LSD) post hoc test to determine the effect of subject specificity and data variability on the reconstruction. We used $P < 0.05$ as a measure of significance for all statistical analyses, which were completed using Statistica (StatSoft, Tulsa, OK) software.

Statistical analysis of synergy recruitment coefficients

To determine the effect of stance configuration on muscle synergy recruitment we first performed a *functional sorting* of control and task-specific muscle synergies across subjects. Muscle synergies of each subject were ordered based on muscle composition and synergy recruitment profiles rather than on percentage of contribution to the total data variability (as in other factorization methods such as principal component analysis). We performed a functional sorting because subjects might use muscle synergies differently, causing comparable muscle synergies to have large differences in contribution to the total data variability.

To perform the functional sorting we computed averaged synergy recruitment coefficients across all trials ($\bar{C}$) for each muscle synergy (W) of each subject. Then an initial sorting was performed by grouping muscle synergies based on the similarity of W values and/or $\bar{C}$ values ($r > 0.70$) to that of an arbitrary reference subject. From this initial sorting, an averaged set of W values and $\bar{C}$ values across subjects was computed. Then, using an iterative process, only muscle synergies that were similar to either averaged W values or $\bar{C}$ values, or both ($r > 0.70$), were kept in the group. The averaged set of W and $\bar{C}$ vectors across subjects were updated every time a muscle synergy was discriminated from a group. The r values obtained served not only as a sorting parameter, but also as a measure to evaluate the generality of muscle synergies across subjects. Therefore within each group, the r values were used to identify similarities across subjects in both W and $\bar{C}$, or only W, or only $\bar{C}$.

Subsequent to the functional sorting, we performed a repeated-measures ANOVA on all sample times of the peak activation for each muscle synergy. Stance condition and time bin were set as factors with Fisher LSD post hoc test to determine the effect of posture and time period on the synergy recruitment coefficients. Bonferroni corrections were done in all our comparisons and we used $P < 0.05$ as a measure of significance for all statistical analyses, which were completed using Statistica software.

RESULTS

In all subjects, both moderate and extreme changes in posture introduced variations in balance responses. Although moderate changes to postural configuration induced mainly changes in EMG amplitude, extreme changes to postural configuration induced changes in both directional and temporal patterning of muscle responses to perturbations. Surprisingly, muscle synergy structures were consistent regardless of the data set from which they were extracted. Control muscle synergies extracted from the normal stance condition reproduced most of the variability in balance responses over both moderate and extreme changes in postural configuration. Under the extreme difference in postural configuration induced by one-leg and crouched stance, some muscle synergies were not restructured and only one additional task-specific muscle synergy was required. Similarities in most muscle synergies were found across subjects, but variability in EMG responses across trials and across conditions was best accounted for by a subject's own muscle synergies rather than those obtained from a different subject.

Changes in muscle activity across postural configurations

Similar to previous studies investigating the effect of stance width (Henry et al. 2001), moderate changes in postural configuration across narrow, normal, and wide stances induce primarily changes in EMG responses amplitude (Fig. 1). Muscle activity decreased as stance width increased, particularly in proximal compared with distal muscles. Both the temporal features (Fig. 1*B*) and the spatial tuning (Fig. 1*C*) of individual muscle activity exhibited similar patterns across moderate changes in postural response.

Across extreme changes in postural configuration in the crouched, one-leg, and widest stances, more complex changes in EMG response amplitude, timing, and spatial tuning were observed (Fig. 1). Changes in amplitude were nonmonotonic in extreme changes to postural configuration, with some muscles increasing and others decreasing their amplitude in response to the same perturbation (Fig. 1*B*). Changes in onset latencies were observed primarily in the crouched stance. In this condition onset latencies of proximal muscles, which normally occurred during APR_2, were activated earlier during APR_1, disrupting the distal-to-proximal muscle activation order typically observed in the normal stance condition (Burtner et al. 1998; Woollacott and Shumway-Cook 2002). Changes in directional tuning of EMG signals were also observed in extreme changes in postural configuration. For example, the directions of maximum and minimum EXOB activity were reversed in widest stance compared with all other conditions (Fig. 1*C*).

Muscle synergies are conserved across postural configurations

In all subjects, control muscle synergies extracted from normal stance were sufficient to account for variations in muscle activity across moderate changes in postural configuration. All subjects had five to seven control muscle synergies (Fig. 4*A*), accounting for 93 ± 1.4, 93 ± 0.8, and 93 ± 1% of the total variability across trials in normal, narrow, and wide stances, respectively. In six of nine subjects, the number of muscle synergies required to reconstruct muscle activity across moderate changes in postural configuration was the same as the number required to reconstruct normal stance only. In the remaining three subjects, we observed the splitting of a muscle synergy extracted from normal stance to account for variation in other stances. In essence, two muscle synergies were controlled together in normal stance, but independently on variation in postural configurations (Clark et al. 2010; Saltiel et al. 2001; Ting et al. 1999).

Task-specific muscle synergies were sometimes needed to account for the variability in two of the extreme configurations: one-leg and crouched stance. Control muscle synergies accounted for 92 ± 1% (widest), 84 ± 9.9% (crouched), and 84 ± 4.7% (one-leg) variability across trials in extreme postural configurations. In contrast to moderate changes in postural configuration, the addition of more control synergies did not improve the VAF values. Task-specific muscle synergies were necessary to account for the variability in one-leg and crouched EMG responses of four or fewer muscles of the 16 that were recorded. The mean VAF in these conditions increased to 91 ± 3.6% (crouched) and 92 ± 1.3% (one-leg) with the addition of a single task-specific muscle synergy for each condition. As an example, in subject 3 we observed that six control muscle synergies constituted the smallest number of synergies that accounted for >75% muscle activity during background and APR periods of all muscles in the narrow, normal, wide, and widest conditions (Fig. 2*A*, red trace). However, not all muscle activity was well reconstructed in the one-legged and crouched stance, as indicated by the poor directional profile of VAF for all time periods (Fig. 2*A*; red trace on one-legged and crouched panels in the second to fourth columns from *right* to *left*) and the low VAF values of REAB, BFLH, and ERSP (Fig. 2*A*; on one-legged and crouched panels in first column on the *right*). Adding one task-specific muscle synergy to the reconstruction of these two conditions dramatically improved the reconstruction of all muscles and the directional profile of VAF (Fig. 2*B*). We did not include more than six control muscle synergies or more than one task-specific muscle synergy in the crouched and one-legged conditions because the addition of further muscle synergies accounted only for the reconstruction of noise, as indicated by similar improvement of VAF values across all perturbation directions for all time periods and muscles (Fig. 2, *A* and *B*, green trace and gray trace, respectively).

Muscle synergies extracted independently from each stance condition were remarkably similar (e.g., Fig. 3). Although not all the control muscle synergies could be extracted from each configuration, the ones that were identified in the test conditions were similar to those extracted in the normal stance. Across subjects, 98, 94, 92, 69, and 67% of the control muscle synergies presented here (e.g., Fig. 3) were also identified when using the narrow data set ($0.81 \pm 0.08 < r < 0.97 \pm 0.02$), the wide data set ($0.86 \pm 0.07 < r < 0.95 \pm 0.04$), the widest data set ($0.81 \pm 0.08 < r < 0.95 \pm 0.03$), the one-leg data set ($0.72 \pm 0.07 < r < 0.94 \pm 0.03$), and the crouched data set ($0.69 \pm 0.12 < r < 0.92 \pm 0.03$), respectively. The fewest numbers of control muscle synergies were extracted from the crouched and one-leg stances because of the low recruitment of control muscle synergies activating proximal muscles. This can be explained by the low activity of trunk muscles in the crouched stance and the low activity of abdominal and hamstring muscles in the one-leg stance. Also in all subjects, control and task-specific muscle synergies presented here (Fig. 3) were similar to muscle synergies extracted from data pooled across all stances ($0.7 \pm 0.07 < r < 0.97 \pm 0.04$) and task-specific synergies were similar to test muscle synergy extracted from the one-leg and crouched stances alone ($r = 0.87 \pm 0.10$). SOL, PERO, VMED, and VLAT were typical examples of muscles in which their overall activation was reproduced by control and task-specific muscle synergies (Fig. 4*B*).

Although the number and muscle synergy structure varied considerably across subjects (Fig. 4), the same muscle synergy structures were consistently extracted from different portions of each subject's data set. Overall, muscle synergies were similar across subjects, although we also observed clear subject-specific differences in muscle synergy structure (Fig. 4, W values on yellow background) or recruitment (Fig. 4, W values on gray background).

The total variability accounted for in each subject's data set was greatest when using subject-specific muscle synergies (Fig. 5). We observed the variance in the data set containing all test conditions was roughly twice that of the normal stance alone (Fig. 5*A*), yet control and task-specific muscle synergies were sufficient to account for these variations. A range of VAF values was obtained when using others' muscle synergies to reconstruct a subject's data. Overall, the goodness in the reconstruction decreased when using others' muscle synergies, as indicated by the significantly lower mean and minimum VAF values (Fig. 5*B*). The poor variability accounted for by others' muscle synergies is also indicated by the low VAF values in the reconstruction of individual muscles (Fig. 5*C*). VAF values in four of nine subjects was <62%, which is approximately the amount of variability accounted for by using artificial muscle synergies extracted from randomly generated

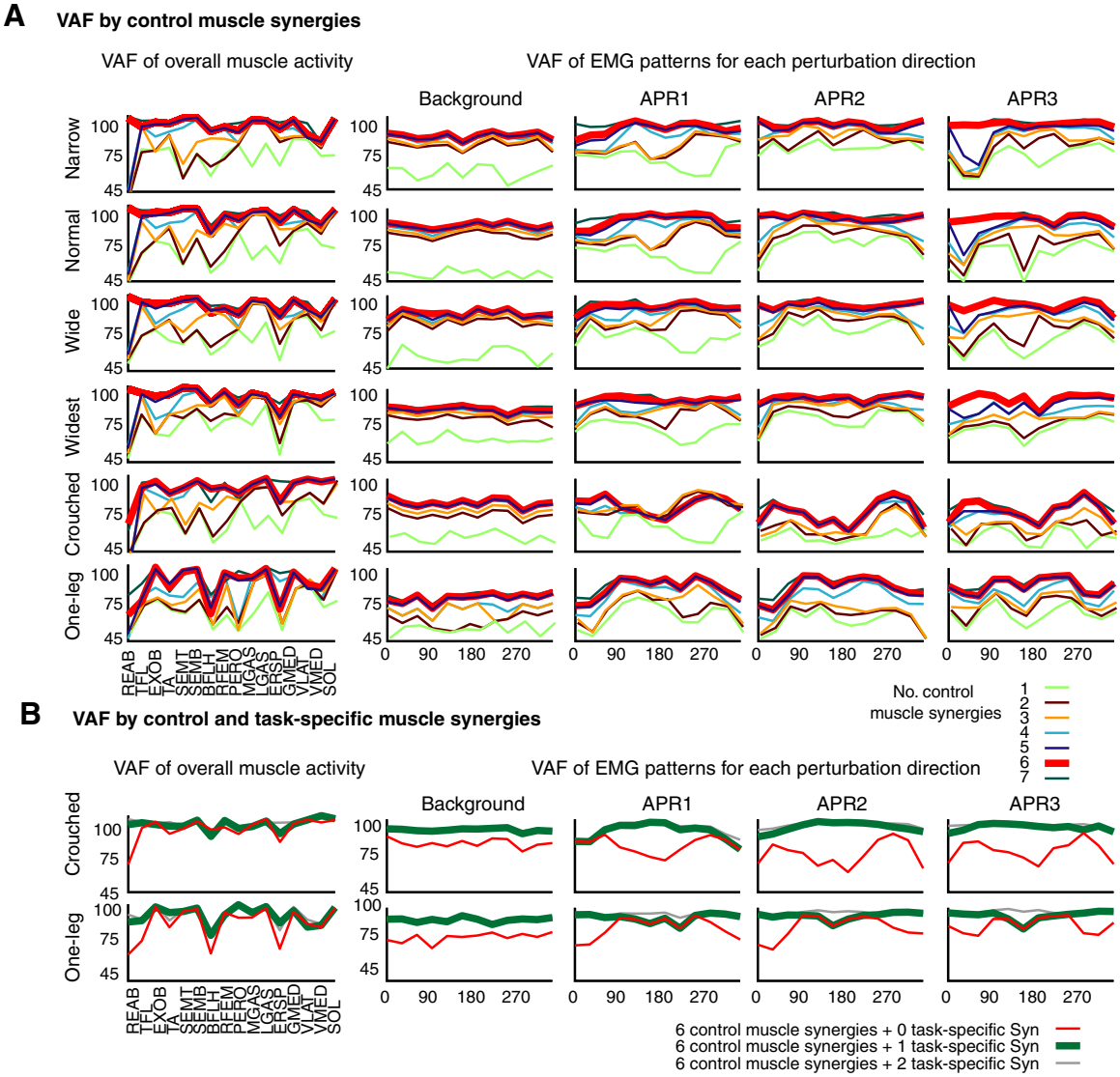

FIG. 2. Variability accounted for (VAF) for each stance condition by using different numbers of muscle synergies in an example subject. Thick lines indicate the number of control and task-specific muscle synergies that were chosen to reconstruct the data of this subject. *A*: VAF values indicating goodness of data reconstruction when control muscle synergies were used to reconstruct EMG responses in all stance conditions. Colored lines indicate the VAF values when different numbers of control muscle synergies were used to reconstruct each muscle's responses across all time bins (1st column) and EMG patterns for all perturbation directions during background (2nd column) and 3 time bins characterizing the APR (3rd to 5th columns) in all stance conditions. Six muscle synergies extracted from the control condition accounted for >75% VAF in all stance conditions except for the crouched and one-legged conditions (red traces). Adding more control muscle synergies evenly improves the VAF values across all perturbation directions and muscle responses (dark green traces), indicating the seventh muscle synergies account for the evenly distributed noise across the data set and should not be included. *B*: VAF when task-specific muscle synergies were included for the data reconstruction. One additional muscle synergy improved the directional profile of VAF in the crouched and one-leg stance conditions (dark green traces). Adding more task-specific muscle synergies accounted only for the reconstruction of noise, as indicated by similar improvement of VAF values across all perturbation directions for all time periods and muscle responses (gray trances) and were therefore not included.

data. Similarities across subjects are revealed by the maximum VAF values, which indicate the best reconstruction values when using another subject's muscle synergies.

Muscle synergy recruitment varies across postures and trials

Variations observed in individual muscle activity when changing standing posture were mediated by changes in recruitment of entire muscle synergies. Changes in control muscle synergies amplitude, directional tuning, and timing are illustrated in sample subject (Fig. 6) and group data analysis (Fig. 7). Across moderate changes in postural configurations, muscle synergies maintained the same preferred directions of recruitment, increasing the level of recruitment as stance narrowed (e.g., Fig. 6, W_1, W_5, and W_6). Only muscle synergy W_3 primarily composed of hamstring muscles increased recruitment level when the stance width increased at the widest stance. These changes in muscle synergy recruitment with stance are reflected in the group data when comparing peak recruitment levels of muscle synergies across stance conditions (Fig. 7). Large changes in the directional tuning of muscle synergies were observed only with extreme changes in posture. For example, in the one-leg and narrow stances, the directional tuning of W_1 and W_6 shifts from anterior–posterior to medial–

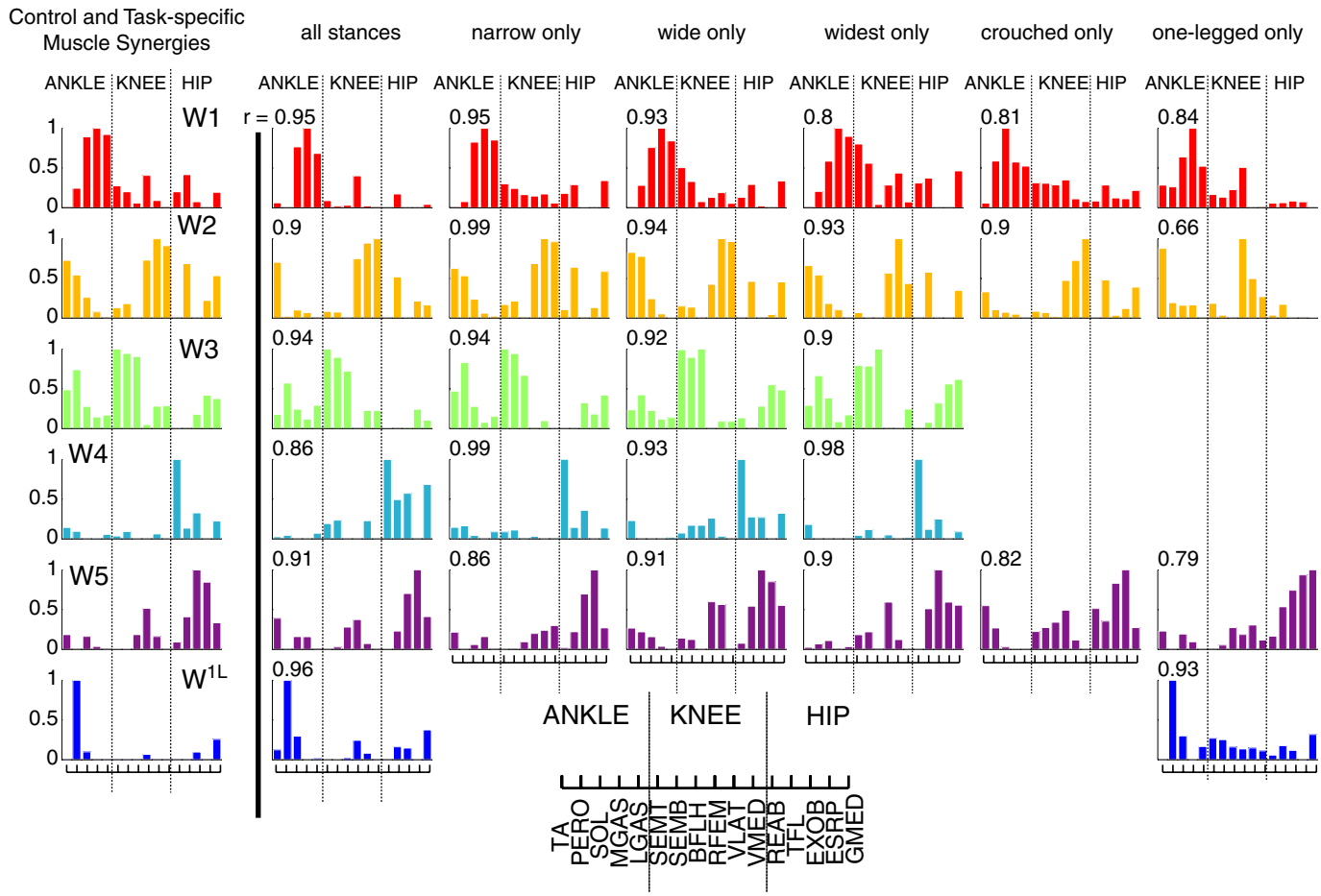

FIG. 3. Muscle synergies extracted from each condition compared with control and task-specific muscle synergies for a sample subject. Five control and one task-specific (W^{1L}) were sufficient to reproduce variability in EMG responses within trials and across all postural configurations. These muscle synergies were compared with muscle synergies extracted from each stance condition alone. Muscle synergies mainly composed of proximal muscles could not be identified in the crouched and one-legged condition in all subjects, when these muscles are not highly recruited. However, all other muscle synergies extracted from each stance were similar to those extracted in the normal stance (e.g., in this subject: $0.66 < r < 0.99$).

lateral directions (Fig. 6, red and dark green). These changes occur, presumably to compensate for the missing contralateral support on medial–lateral perturbations.

Significant temporal differences in the recruitment of muscle synergies was mainly observed in the extreme stance conditions ($P < 0.001$). Temporal patterns of muscle synergies recruitment by either starting at an earlier onset (e.g., C_2 in the crouched stance), later onset (e.g., C_4 in the widest stance), or increasing their background activity (e.g., C_6 in the one-leg stance). For example, the onset of C_2, which recruited a muscle synergy that was largely composed by quadriceps muscles, changed to an earlier time bin APR_1 in the crouched stance. Changes in background activity of muscle synergies were mainly observed in the extreme stance conditions, such as the larger recruitment level in C^{Cr} and C_2 in the crouched stance and C_6, formed by ankle dorsiflexor and evertors and biarticular muscle biceps femoris, in the one-leg stance.

In all stance conditions, intertrial variations in EMG activity of individual muscles were not due to noise at the level of muscles, but instead corresponded to intertrial variations in the recruitment of entire muscle synergies. Similar trial-to-trial variations of responses were observed in two trials of stances with very different biomechanical stability conditions: the one-leg and wide stances (Fig. 8, black dots). The changes in activation of individual muscles, however, were accompanied by similar changes in the activation of all other muscles belonging to W_2 (Fig. 8, yellow bars). Therefore intertrial changes in muscle magnitude were not simply a random variation in individual muscle activity but corresponded to modulation of an entire muscle synergy from one trial with respect to another.

Although we observed variability in muscle synergy recruitment within each stance, the average contribution of each muscle synergy to balance responses across stances was very consistent (Fig. 9). That is, the relative contribution of muscle synergies indicated by the VAF level per muscle synergy is very similar in the narrow, normal, wide, and widest stances. These results not only indicate that all control muscle synergies were recruited in all stances but that they were recruited similarly, suggesting there might also be constraints on the recruitment of muscle synergies to EMG responses for balance control. These patterns of muscle synergy recruitment were shifted in the one-leg and crouched conditions (Fig. 9).

DISCUSSION

Because muscle synergy structures were consistent across different postural configurations, it is unlikely that they were

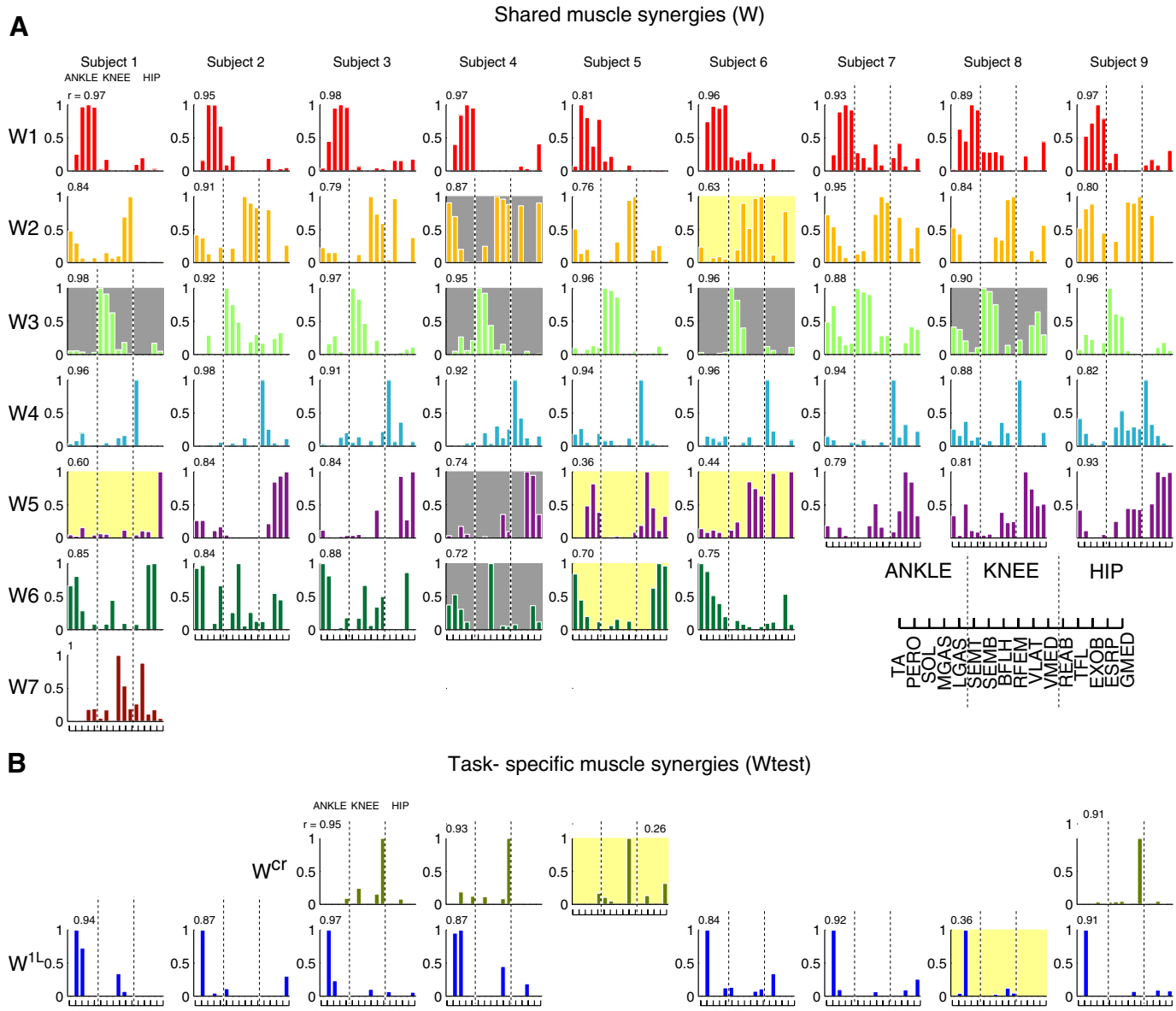

FIG. 4. Control and task-specific muscle synergies for all subjects. *A*: 5 to 7 control muscle synergies were extracted from the normal stance data set in each subject. These muscle synergies were sufficient to reproduce variability in EMG responses within trials and across all postural configurations. Muscle synergies are grouped by similarities across subjects. However, differences in muscle synergy composition (*W* values on yellow background) and synergy recruitment coefficients (*W* values on gray background) were observed in some subjects. Muscle activation patterns specified by each muscle synergy were consistently identified in each subject's EMG responses across all stance conditions. *B*: all subjects required at least one task-specific muscle synergies to reproduce muscle activation patterns of selected muscles in the crouched or one-leg conditions.

emergent from the optimal control of a particular musculoskeletal configuration, nor from the pattern of multisensory inflow at the time of perturbation. Our results demonstrate that changes in muscle coordination across postural configurations can be reproduced by changing the level of recruitment of a consistent set of subject-specific muscle synergies. In balance tasks with very different demands such as standing on one leg or crouching, one additional task-specific muscle synergy was activated in addition to the preexisting ones, but de novo muscle synergies were not generated. Moreover, trial-by-trial variability observed within a biomechanical context was also constrained within the muscle synergy manifold, suggesting that intertrial EMG changes arise from changes in muscle synergy recruitment and not to random changes in individual muscle activity. The consistency of muscle synergy structures for balance across postural configurations, which would induce different somatosensory patterns, but require similar task goals, supports the idea that muscle synergies are indeed consistent motor modules to map intention to action. Our results suggest that a repertoire of motor tasks is achieved through the modulation of muscle synergy recruitment but not muscle synergy structure.

The consistency in muscle synergy structures across postural configurations suggests that the low-dimensionality of muscle activity does not emerge from optimal control solutions generated for each condition. Subjects continued using the same set of muscle synergies for balance control in extreme changes in postural configuration, whereas optimal control models would predict muscle synergies to change as biomechanical parameters such as joint angles, muscle lengths, and moment

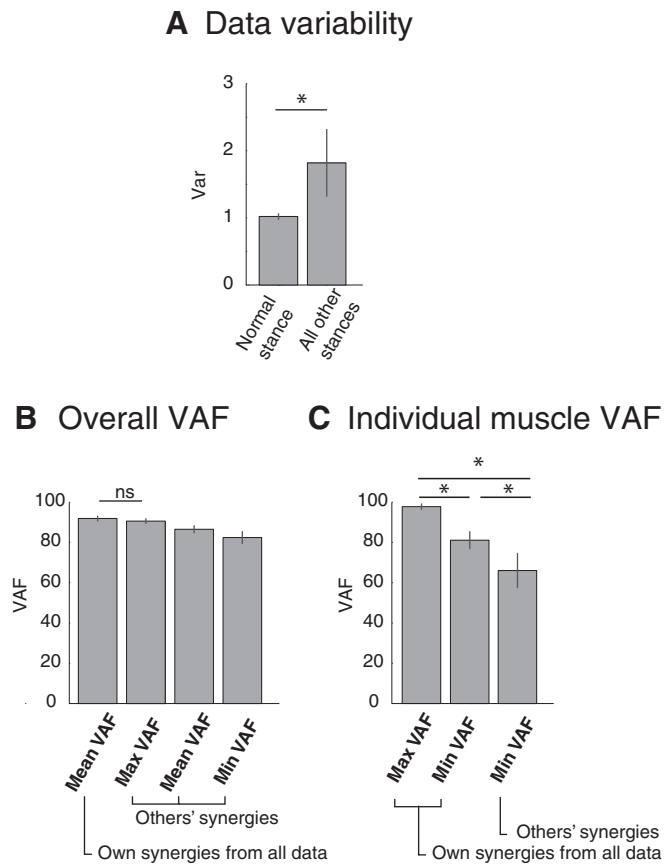

FIG. 5. Variability in muscle activation patterns and percentage VAF by muscle synergies extracted from *1*) each subject's own trials in normal stance and *2*) other subjects' EMG responses in normal stance. *A*: variance in the muscle activation patterns in the pooled test conditions is significantly larger than that in the normal stance, from which control muscle synergies were extracted. *B*: when accounting for total variability across all muscles and conditions, similar reconstruction levels were possible when using muscle synergies from another subject. However, the mean and minimum variabilities accounted for were significantly decreased when using another subject's muscle synergies. *C*: variability accounted for in individual muscles is a more sensitive indicator of the goodness of fit and the minimum VAF was significantly lower when using other subject's muscle synergies.

arms changed (Hamilton et al. 2004; Kurtzer et al. 2006). Moreover, when additional biomechanical functions were necessary, such as the production of medial forces during the one-leg condition, subjects added an additional muscle synergy, rather than reshaping all muscle synergies. Our findings are consistent with evidence demonstrating that muscle synergies are preserved across biomechanically different loading conditions, postural configurations, and locomotor tasks (Cheung et al. 2009a; d'Avella and Bizzi 2005; Torres-Oviedo et al. 2006). This suggests that for a given motor task, the nervous system recruits preexisting muscle synergies rather than generating a specific optimal solution for each condition (Chhabra and Jacobs 2006; Scott 2004; Todorov and Ghahramani 2004a). Muscle synergies may therefore be optimal when considering an entire movement repertoire, rather than being specific to a particular movement condition or limb configuration (Berniker et al. 2009; McKay and Ting 2008). It remains to be investigated whether optimization processes determine how new muscle synergies are developed in the face of new task demands and whether preexisting muscle synergies represent the starting point for learning task-specific muscle synergies.

The fact that differences in sensory inflow in different postural configuration alter only the recruitment of muscle synergies and not their structure suggests that they reflect modularity in motor modules and that are not patterned by sensory inflow. However, we show that differences in sensory inflow may alter the recruitment of muscle synergies. This is consistent with postural control studies demonstrating that muscle stretch is not always predictive of muscle activations for balance control (Carpenter et al. 1999; Horak and Nashner 1986; Nashner 1977; Ting and Macpherson 2004). Similarly, our previous work in feline postural control demonstrated that the same muscle synergies were recruited when opposite joint angle disturbances were induced (Torres-Oviedo et al. 2006). The idea that muscle synergies are motor modules is further supported by the observation that deafferentation does not alter muscle synergy structure but only their recruitment (Cheung et al. 2005; Kargo et al. 2010).

The fact that subject-specific muscle synergies were consistent across days and across postural configurations suggests that they may reflex habitual or heuristic motor solutions encoded in the nervous system. Although the biomechanics of the musculoskeletal system imposes constraints on muscle coordination patterns (Kutch et al. 2008; Valero-Cuevas 2000), individual differences in morphology are unlikely to account for all of the subject-specific differences in muscle synergy number and structure. Because of the musculoskeletal redundancy, multiple solutions for any given biomechanical task exist (Bernstein 1967). Specific to standing balance control, we have demonstrated that a high degree of flexibility in muscle activation patterns remains when the biomechanical constraints of standing are imposed (Bunderson et al. 2008). The similarities in muscle synergy tuning curves across subjects provide evidence that similar task constraints are imposed on all subjects when the CoM is perturbed in various directions. However, individual differences in the specific patterns of muscle activity used to achieve those tasks can vary considerably (Torres-Oviedo and Ting 2007; Torres-Oviedo et al. 2006). These differences might be due to the influence of training and experience, which would affect the range of behaviors that are used to tailor the specific structure of muscle synergies in an individual. A similar phenomenon has been observed in neuronal circuit models, demonstrating not only the necessity of using subject-specific parameter sets rather than parameter values averaged across subjects (Golowasch et al. 2002) but also the wide range of possible parameter sets that generate similar behavioral outcomes (Prinz et al. 2004). Moreover, recent work suggests that motor cortex topological organization reflects muscle coordination patterns that are most dominant in the behavioral repertoire (Aflalo and Graziano 2006, 2007; Graziano and Aflalo 2007), which indicates the possibility for experience-dependent and subject-specific shaping of muscle synergies.

There is no clear consensus of where muscle synergies may be encoded in the CNS and how they are modulated. Muscle synergies for frog wiping reflexes may be encoded in spinal centers, as shown by the consistent modular motor activity in the frog on spinal stimulation (Hart and Giszter 2010; Saltiel et al. 2001). Muscle synergies for locomotion and scratching may also be located in spinal networks that are recruited by rhythm-

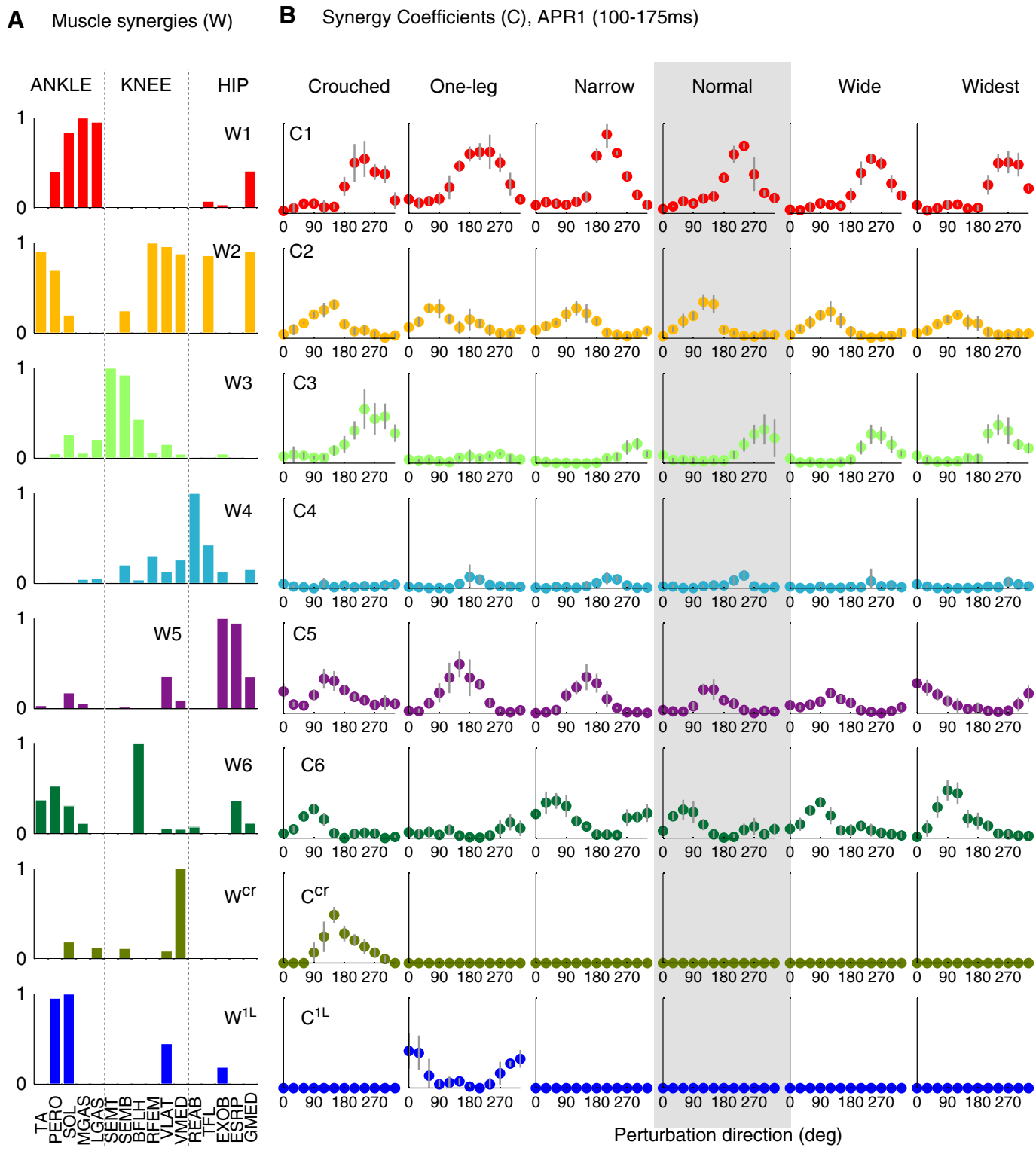

FIG. 6. Mean (±SD) synergy recruitment levels across stance configurations in a representative subject. *A*: control muscle synergy vectors W_i, extracted from EMG responses in normal stance, and task-specific muscle synergies for crouched W^{Cr} and one-leg W^{1L} stance condition. Each bar represents the relative level of activation of each muscle within the synergy (see METHODS section for muscle abbreviations). Task-specific muscle synergies are mainly formed by a highly activated muscle. *B*: mean muscle synergy tuning curves during APR_1. The mean recruitment level of control muscle synergies C_i and task-specific muscle synergies C^{test} vary as a function of perturbation direction. The spatial tuning of muscle synergy recruitment was consistent across moderate changes in postural configuration (narrow, normal, wide stances) but could shift in extreme changes in postural configuration (crouched, one-leg, widest stances).

generating circuits (McCrea and Rybak 2008). On the other hand, muscle synergies for posture and balance control may be mediated by brain stem nuclei. Reticulospinal neurons (RSNs) project to multiple motoneuronal pools and RSNs are activated during postural adjustments across different behavioral and biomechanical contexts (Schepens and Drew 2004, 2006;

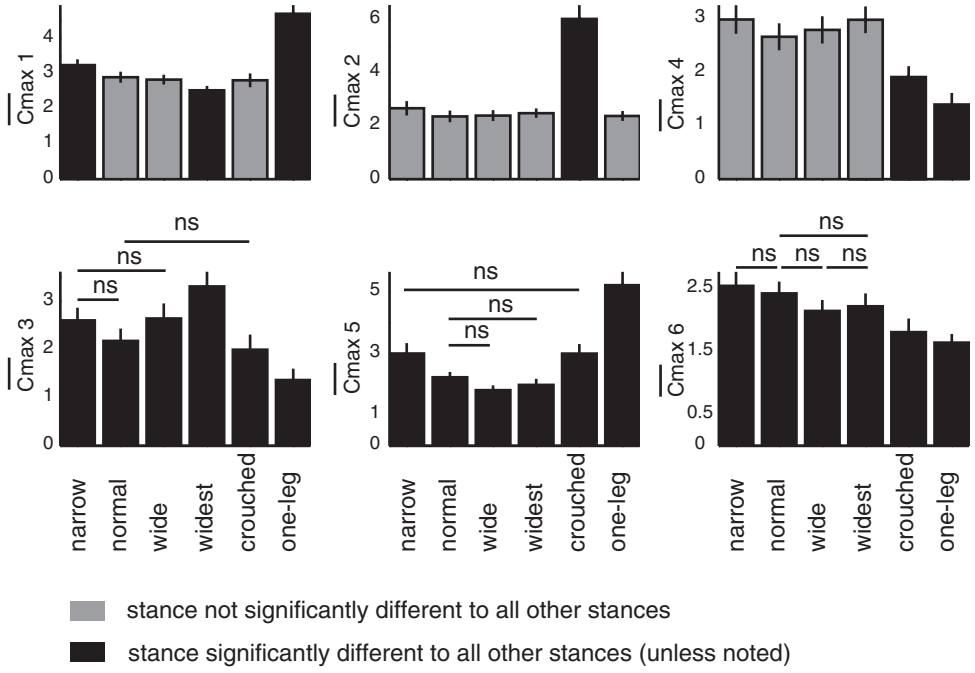

FIG. 7. Mean peak levels in muscle synergy recruitment in all postural configurations averaged across all subjects. Consistent changes in the recruitment of muscle synergies were observed across postural configurations in all subjects (black bars denote significant differences across all conditions except where noted by *ns*).

Schepens et al. 2008; Stapley and Drew 2009). Damage to the cerebrum following stroke has recently been shown to impair the independent recruitment of muscle synergies but not their structure in either walking or reaching (Cheung et al. 2009b; Clark et al. 2010), suggesting that muscle synergies are not encoded by cerebral projections to motorneuronal pools.

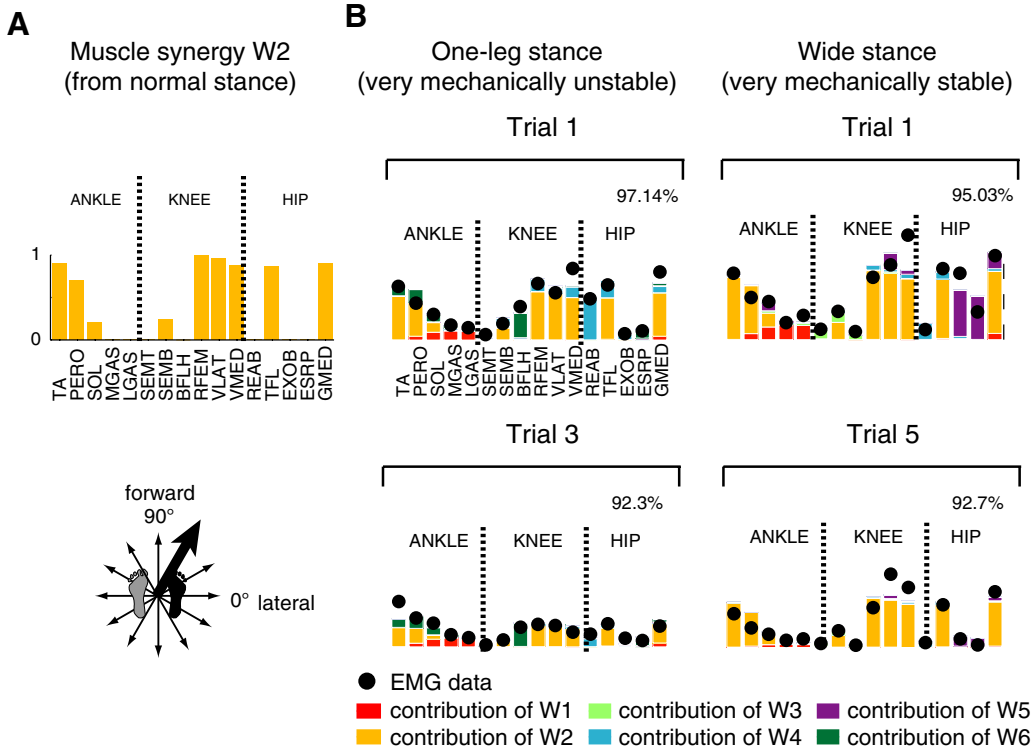

FIG. 8. Example of muscle synergy contributions to trial-by-trial variations in muscle activation patterns within and across postural configurations. *A*: example control muscle synergy extracted from normal stance. *B*: reconstruction example of muscle activation patterns (black dots) in 4 postural response trials collected in 2 very different stance configurations. Black dots indicate the level of muscle activity elicited in time bin 1 during each trial. The magnitude of the colored bars represents the contribution of each muscle synergy to the postural response across all muscles. This figure illustrates how W_2, representing a multimuscle pattern identified in the normal stance, is also identified in EMG responses in conditions with very different mechanical stability: the one-legged and wide stance. This figure also shows that from one trial to the next the whole muscle synergy changes its activity and not just individual muscles within the muscle synergy. Trial-to-trial variations in EMG responses result from variations in muscle synergy recruitment, modulating the entire pattern of muscle activity across multiple muscles. For example, all muscles activated by muscle synergy W_2 (yellow bars) increase in trial 1 of the one-leg condition and decrease in trial 3. Similar observations can be made in the wide stance condition.

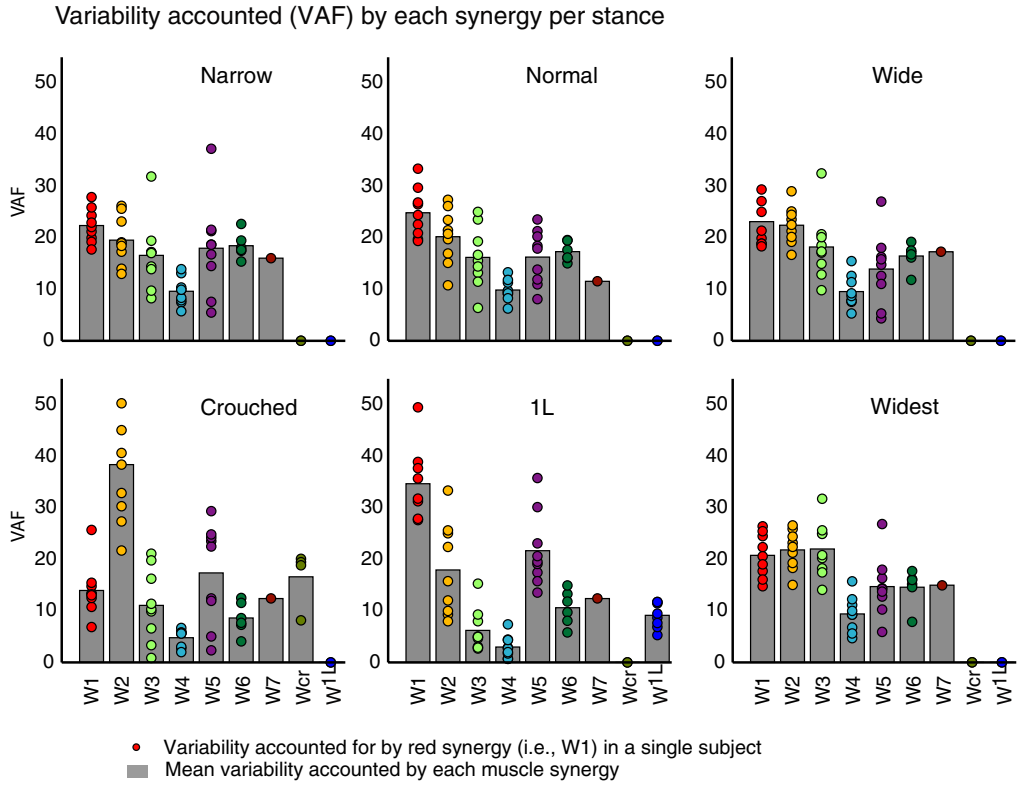

FIG. 9. Muscle synergy contributions to EMG responses at each stance configuration averaged across subjects. Muscle synergies are recruited differently across subjects, as shown by the spread in colored dots indicating the mean contribution of each synergy in a particular subject in each condition. However, similar recruitment profiles of muscle synergies were observed for the narrow, normal, wide, and widest stance. Although most of the muscle synergies contribute to the EMG responses in the crouched and one-leg stances, the recruitment profiles of muscle synergies are very different from those observed in the other stances.

Rather, cortical projections may modulate muscle synergy recruitment. Accordingly, projections from motor cortex to multiple motoneuronal pools for reaching (Holdefer and Miller 2002; Schwartz et al. 1988) have been shown to change their level of recruitment as a function of postural configuration (Kakei et al. 1999; Scott and Kalaska 1997). Moreover, stimulation of different cortical sites can recruit similar low-dimensional hand movements (Gentner and Classen 2006).

Intertrial variations in muscle synergy recruitment may be explained by variations in activity of hierarchal neural structures regulating movement. Recent studies demonstrate that variability in the firing of premotor structures is correlated to trial-by-trial variability in behavioral features such as pitch in birdsong (Sober et al. 2008), reaching speed in monkeys (Churchland et al. 2006), and eye movement in monkeys (Medina and Lisberger 2007). Variability in motor output may therefore be centrally controlled and passed to the behavior through downstream sensorimotor transformations (Soechting and Flanders 2008; Yanai et al. 2008) of reduced dimension (Flash and Hochner 2005; Lockhart and Ting 2007). Similarly, intertrial variations in muscle synergy activations might arise from descending influences such as expectation, habituation, or emotion, which are factors that have been shown to affect EMG responses (Carpenter et al. 2004; Woollacott and Shumway-Cook 2002). Alternately, the influence of biomechanical context in muscle synergy recruitment that we observe could explain the intertrial variations in EMG patterns. It is possible that trial-by-trial variations were due to small variations in biomechanical configuration at the onset of the perturbations, since we did not strictly regulate the initial postural configuration of the subject. Likewise, it is possible that the trial-by-trial variations we observed were due to small differences in the sensory inflow arising from small variations in biomechanical configuration from one trial to the next.

Why are muscle synergies useful?

Muscle synergies may provide a simplifying mechanism for muscle coordination, not because they reduce the number of variables controlled by the nervous system, but because they map high-level task goals into actions. Control of task-level variables by muscle synergies has been identified in reaching studies showing modular control of limb endpoint forces (Georgopoulos et al. 1992) or endpoint motions (Holdefer and Miller 2002; Schwartz et al. 1988; Scott and Kalaska 1997). In balance control, this mapping would allow standing balance through the control of encoded task variables rather than individual muscles. Accordingly, muscle activity in balance control is modulated over time in response to changes in CoM kinematics rather than individual joint motions (Lockhart and Ting 2007; Welch and Ting 2008). Moreover, we have found consistent relationships between the recruitment of muscle synergies and the modulation of endpoint forces across postural configurations (Torres-Oviedo et al. 2006). Thus the nervous system might use these relationships to reliably coordinate the redundant structures of the limb across different biomechanical contexts. Muscle synergies controlling task variables would thus allow for the rapid reconfiguration of muscle coordination patterns in a context-dependent manner. This idea is analogous to the concepts in sparse coding of

sensory inputs (Olshausen and Field 2004), where representations of images are based on a small set of basis functions selected from a large library. Therefore a few muscle synergies may be controlled by the nervous system in any given motor behavior, but a whole library of muscle synergies may be available for the construction of movements (Chiel et al. 2009; McKay et al. 2007). Muscle synergies may therefore provide a consistent mapping between task-level and execution-level control of balance. Such a modular organization may be advantageous in reducing the number of output variables that are modulated during the rapid adaptation to changing task demands (Fiete et al. 2004; McKay et al. 2007), by providing faster convergence to new solutions during learning (Chhabra and Jacobs 2006; Todorov and Ghahramani 2004b). Using motor modules that define task-level actions may therefore be advantageous for the adaptive neural control of movement.

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DISCLOSURES

No conflicts of interest are declared by the authors.

REFERENCES

Aflalo TN, Graziano MSA. Possible origins of the complex topographic organization of motor cortex: reduction of a multidimensional space onto a two-dimensional array. *J Neurosci* 26: 6288–6297, 2006.

Aflalo TN, Graziano MSA. Relationship between unconstrained arm movements and single-neuron firing in the macaque motor cortex. *J Neurosci* 27: 2760–2780, 2007.

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.

Bernstein N. *The Coordination and Regulation of Movements.* New York: Pergamon Press, 1967.

Bunderson NE, Burkholder TJ, Ting LH. Reduction of neuromuscular redundancy for postural force generation using an intrinsic stability criterion. *J Biomech* 41: 1537–1544, 2008.

Burtner PA, Qualls C, Woollacott MH. Muscle activation characteristics of stance balance control in children with spastic cerebral palsy. *Gait Posture* 8: 163–174, 1998.

Carpenter MG, Allum JHJ, 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.

Carpenter MG, Frank JS, Adkin AL, Paton A, Allum JH. Influence of postural anxiety on postural reactions to multi-directional surface rotations. *J Neurophysiol* 92: 3255–3265, 2004.

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, 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.

Cheung VCK, 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.

Chhabra M, Jacobs RA. Properties of synergies arising from a theory of optimal motor behavior. *Neural Comput* 18: 2320–2342, 2006.

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.

Churchland MM, Santhanam G, Shenoy KV. Preparatory activity in premotor and motor cortex reflects the speed of the upcoming reach. *J Neurophysiol* 96: 3130–3146, 2006.

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.

Diener HC, Horak FB, Nashner LM. Influence of stimulus parameters on human postural responses. *J Neurophysiol* 59: 1888–1905, 1988.

Fagg AH, Shah A, Barto AG. A computational model of muscle recruitment for wrist movements. *J Neurophysiol* 88: 3348–3358, 2002.

Fiete IR, Hahnloser RHR, Fee MS, Seung HS. Temporal sparseness of the premotor drive is important for rapid learning in a neural network model of birdsong. *J Neurophysiol* 92: 2274–2282, 2004.

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

Gentner R, Classen J. Modular organization of finger movements by the human central nervous system. *Neuron* 52: 731–742, 2006.

Georgopoulos AP, Ashe J, Smyrnis N, Taira M. The motor cortex and the coding of force. *Science* 256: 1692–1695, 1992.

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.

Golowasch J, Goldman MS, Abbott LF, Marder E. Failure of averaging in the construction of a conductance-based neuron model. *J Neurophysiol* 87: 1129–1131, 2002.

Graziano MS, Aflalo TN. Rethinking cortical organization: moving away from discrete areas arranged in hierarchies. *Neuroscientist* 13: 138–147, 2007.

Hamilton AF, Jones KE, Wolpert DM. The scaling of motor noise with muscle strength and motor unit number in humans. *Exp Brain Res* 157: 417–430, 2004.

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

Henry SM, Fung J, Horak FB. EMG responses to maintain stance during multidirectional surface translations. *J Neurophysiol* 80: 1939–1950, 1998.

Henry SM, Fung J, Horak FB. Effect of stance width on multidirectional postural responses. *J Neurophysiol* 85: 559–570, 2001.

Holdefer RN, Miller LE. Primary motor cortical neurons encode functional muscle synergies. *Exp Brain Res* 146: 233–243, 2002.

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, 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.

Kakei S, Hoffman DS, Strick PL. Muscle and movement representations in the primary motor cortex. *Science* 285: 2136–2139, 1999.

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.

Kurtzer I, Pruszynski JA, Herter TM, Scott SH. Primate upper limb muscles exhibit activity patterns that differ from their anatomical action during a postural task. *J Neurophysiol* 95: 493–504, 2006.

Kutch JJ, Kuo AD, Bloch AM, Rymer WZ. Endpoint force fluctuations reveal flexible rather than synergistic patterns of muscle cooperation. *J Neurophysiol* 100: 2455–2471, 2008.

Lee DD, Seung HS. Algorithms for non-negative matrix factorization. *Adv Neural Info Proc Syst* 13: 556–562, 2001.

Lockhart DB, Ting LH. Optimal sensorimotor transformations for balance. *Nat Neurosci* 10: 1329–1336, 2007.

McCrea DA, Rybak IA. Organization of mammalian locomotor rhythm and pattern generation. *Brain Res Rev* 57: 134–146, 2008.

McGowan CP, Neptune RR, Clark DJ, Kautz SA. Modular control of human walking: adaptations to altered mechanical demands. *J Biomech* 43: 412–419, 2010.

McKay JL, Burkholder TJ, Ting LH. Biomechanical capabilities influence postural control strategies in the cat hindlimb. *J Biomech* 40: 2254–2260, 2007.
McKay JL, Ting LH. Functional muscle synergies constrain force production during postural tasks. *J Biomech* 41: 299–306, 2008.
Medina JF, Lisberger SG. Variation, signal, and noise in cerebellar sensory-motor processing for smooth-pursuit eye movements. *J Neurosci* 27: 6832–6842, 2007.
Nashner LM. Fixed patterns of rapid postural responses among leg muscles during stance. *Exp Brain Res* 30: 13–24, 1977.
Neptune RR, Clark DJ, Kautz SA. Modular control of human walking: a simulation study. *J Biomech* 42: 1282–1287, 2009.
Olshausen BA, Field DJ. Sparse coding of sensory inputs. *Curr Opin Neurobiol* 14: 481–487, 2004.
Overduin SA, d'Avella A, Roh J, Bizzi E. Modulation of muscle synergy recruitment in primate grasping. *J Neurosci* 28: 880–892, 2008.
Prinz AA, Bucher D, Marder E. Similar network activity from disparate circuit parameters. *Nat Neurosci* 7: 1345–1352, 2004.
Raasch CC, Zajac FE. Locomotor strategy for pedaling: muscle groups and biomechanical functions. *J Neurophysiol* 82: 515–525, 1999.
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, Drew T. Independent and convergent signals from the pontomedullary reticular formation contribute to the control of posture and movement during reaching in the cat. *J Neurophysiol* 92: 2217–2238, 2004.
Schepens B, Drew T. Descending signals from the pontomedullary reticular formation are bilateral, asymmetric, and gated during reaching movements in the cat. *J Neurophysiol* 96: 2229–2252, 2006.
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.
Schwartz AB, Kettner RE, Georgopoulos AP. Primate motor cortex and free arm movements to visual targets in three-dimensional space. I. Relations between single cell discharge and direction of movement. *J Neurosci* 8: 2913–2927, 1988.
Scott SH. Optimal feedback control and the neural basis of volitional motor control. *Nat Rev Neurosci* 5: 534–546, 2004.
Scott SH, Kalaska JF. Reaching movements with similar hand paths but different arm orientations. I. Activity of individual cells in motor cortex. *J Neurophysiol* 77: 826–852, 1997.
Sober SJ, Wohlgemuth MJ, Brainard MS. Central contributions to acoustic variation in birdsong. *J Neurosci* 28: 10370–10379, 2008.
Soechting JF, Flanders M. Sensorimotor control of contact force. *Curr Opin Neurobiol* 18: 565–572, 2008.
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, 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. 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.
Todorov E, Ghahramani Z. Analysis of the synergies underlying complex hand manipulation. *Conf Proc IEEE Eng Med Biol Soc* 6: 4637–4640, 2004a.
Todorov E, Ghahramani Z. Unsupervised learning of sensory-motor primitives. In: *Proceedings of the 26th Annual International Conference of the IEEE Engineering Medicine and Biology Society*. Piscataway, NJ: IEEE, 2004b, p. 1750–1753.
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.
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, Jarc A. The case for and against muscle synergies. *Curr Opin Neurobiol* 19: 601–607, 2009.
Tropp H, Odenrick P. Postural control in single-limb stance. *J Orthop Res* 6: 833–839, 1988.
Valero-Cuevas FJ. Predictive modulation of muscle coordination pattern magnitude scales fingertip force magnitude over the voluntary range. *J Neurophysiol* 83: 1469–1479, 2000.
Valero-Cuevas FJ, Zajac FE, Burgar CG. Large index-fingertip forces are produced by subject-independent patterns of muscle excitation. *J Biomech* 31: 693–703, 1998.
Welch TD, Ting LH. A feedback model reproduces muscle activity during human postural responses to support-surface translations. *J Neurophysiol* 99: 1032–1038, 2008.
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.
Yanai Y, Adamit N, Israel Z, Harel R, Prut Y. Coordinate transformation is first completed downstream of primary motor cortex. *J Neurosci* 28: 1728–1732, 2008.
Zar JH. *Biostatistical Analysis*. Upper Saddle River, NJ: Prentice-Hall, 1999.