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Synergies and motor equivalence in voluntary sway tasks: The effects of visual and mechanical constraints

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Abstract

We used two analyses developed within the framework of the uncontrolled manifold hypothesis to quantify multi-muscle synergies during voluntary body sway: Analysis of inter-trial variance and analysis of motor equivalence with respect to the center of pressure (COP) trajectory. Subjects performed voluntary sway tasks in the anterior-posterior direction at 0.33 and 0.66 Hz. Muscle groups (M-modes) were identified in the space of muscle activations and used as elemental variables in the synergy analyses. Changing mechanical and vision-feedback-based constraints led to significant changes in indices of sway performance such as COP deviations in the uninstructed, medio-lateral direction and indices of spontaneous postural sway. In contrast, there were no significant effects on synergy indices. These findings show that the neural control of performance and of its stability may involve different control variables and neurophysiological structures. There were strong correlations between the indices of motor equivalence and those computed using the inter-cycle variance analysis. This result is potentially important for studies of patients with movement disorders who may be unable to perform multiple trials (cycles) at any given task, making analysis of motor equivalence of single trials a viable alternative to explore changes in stability of actions.

Keywords

motor equivalence; motor variability; posture; synergy; uncontrolled manifold; visual feedback

Introduction

Multi-muscle coordination during whole-body tasks has been viewed as based on neural organization of muscles into groups addressed as *synergies* or *modes* (D'Avella et al. 2003; Krishnamoorthy et al. 2003a; Ivanenko et al. 2004; Ting and Macpherson 2005). According to the traditional view, the main purpose of this organization is to alleviate the problem of

motor redundancy (Bernstein 1967) by using one neural control variable per group of muscles. This is expected to lead to a relatively low-dimensional space where the control and coordination can be examined. Within the idea of motor abundance (Gelfand and Latash 1998; Latash 2012), the problem of motor redundancy is only apparent, and the central nervous system uses large, abundant, sets of elements to ensure stable performance of salient, task-specific variables. This approach accepts the idea of organizing muscles into groups and then views such groups as elemental variables, a space within which synergies are organized stabilizing task-specific performance variables. We will address such muscle groups as muscle modes (M-modes, Krishnamoorthy et al. 2003a) to avoid confusion with synergies stabilizing performance. M-modes are viewed not as a method of alleviating the problem of redundancy but as a reflection of the neural control with a set of elemental changes in referent body configurations (reviewed in Latash 2008, 2010; Feldman 2015).

This approach to the problem of postural stability is not the only one. Keeping vertical posture has been viewed as the problem of stabilizing an inverted pendulum (Winter et al. 1996) with the help of sensory-based feedback loops. This approach has faced several problems. First, experimental estimations of the apparent ankle joint stiffness have produced conflicting results, typically much lower than those necessary to stabilize the inverted pendulum representing the body (Morasso and Sanguineti 2002; Casadio et al. 2005). In addition, it has been shown that the length of muscle fibers may change in the opposite direction to what could be concluded by observation of joint motion (Loram et al. 2005). Nevertheless, schemes based on the control theory are still influential; they are sometimes rather complex involving several loops acting in parallel driven by sensory signals of different modalities (Maurer et al. 2006; Goodworth and Peterka 2012). Our approach may be viewed as based not on the control theory but on physics, i.e., search for laws of nature that define observed behaviors including their stability properties (Latash 2016).

Multi-muscle synergies have been studied within the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999; reviewed in Latash et al. 2007). One of the methods developed within this approach quantifies inter-trial (or inter-cycle, in cyclical tasks) variance in the M-mode space within two sub-spaces. One of them corresponds to no change in a salient performance variable; it represents the UCM for that variable. The other (ORT) is orthogonal to the UCM. If variance within the UCM is larger than within ORT ($V_{\text{UCM}} > V_{\text{ORT}}$, both quantified per degree-of-freedom), a conclusion is drawn that a multi-mode synergy stabilizes that performance variable. This method requires collecting multiple trials to have reliable estimates of the variance indices. As a result, its application to clinical studies of multi-muscle systems has been limited (Falaki et al. 2016, 2017).

A complementary method has been recently developed to estimate stability of performance variables in multi-dimensional spaces; this method does not require collecting numerous trials (Scholz et al. 2007; Mattos et al. 2011, 2013, 2015). It quantifies the magnitude of deviations along the UCM and ORT spaces during actions. Deviation along the UCM has been addressed as motor equivalent (ME), while deviation along ORT has been addressed as non-motor equivalent (nME). So far, this method has not been applied to analysis of muscle activations in whole-body tasks.

This study had three main goals. First, we explored the two methods of estimating stability of a salient performance variable, such as the center of pressure coordinate in the anterior-posterior direction (COP_{AP}), during voluntary sway tasks. The first method was based on estimating V_{UCM} and V_{ORT} and the second one – on estimating ME and nME motions. Note that the two methods quantify different characteristics of motion in the space of elemental variables, variance structure across all cycles and displacements from a cycle to a cycle. Based on statistical considerations (see in more detail in Discussion) and assumed normal distributions of the data, we hypothesized that $\sqrt{V_{UCM}}$ would correlate with ME and $\sqrt{V_{ORT}}$ would correlate with nME (Hypothesis 1).

Second, we also explored the effects of mechanical and visual constraints on the task performance and multi-mode synergies stabilizing the COP_{AP} trajectory. Based on earlier studies exploring a range of challenging factors during whole-body sway tasks (Danna-dos-Santos et al. 2007, 2008; Asaka et al. 2008), we expected to see a drop in the amount of variance in the muscle activation space accounted for by a fixed number of M-modes and weaker synergies under the conditions with challenging mechanical constraints, reflected in both V_{UCM}/V_{ORT} and ME/nME analyses (Hypothesis 2A). We expected smaller effects of visual constraints compared to mechanical constraints (Hypothesis 2B) based on earlier studies that documented different effects of natural and virtual (visually defined) tasks on multi-digit synergies (Solnik et al. 2015, 2016).

Third, we also explored the effects of changing sway speed on synergies. Based on earlier studies, we expected an increase in both V_{UCM} and V_{ORT} (cf. Danna-dos-Santos et al. 2007) during faster actions without a change in the relative amount of each of the variance indices. Based on the assumed correlations between the $\{V_{UCM}; V_{ORT}\}$ and $\{ME; nME\}$ indices, we also expected an increase in both ME and nME components with sway speed (Hypothesis 3).

Methods

Participants

Twelve healthy participants, five females and seven males (age 25.3 ± 5.4 years old, body mass 71.9 ± 17.6 kg, height 1.75 ± 0.11 m; mean $\pm$ SD), without any neurological, muscular, and/or orthopedic conditions took part in this study. All participants signed informed consent prior to the study, which was approved by the Office for Research Protections of the Pennsylvania State University. Ten participants were right-leg dominant and the other two did not show leg dominance based on their preferred leg for kicking a ball.

Apparatus

A force platform (AMTI, OR-6) was used to record three forces (F_X, F_Y, F_Z) as well as their moments of forces (M_X, M_Y, M_Z). The force plate coordinate system was defined with the X -axis pointing forward, along the anterior-posterior (AP) direction, the Y -axis pointing to the right, along the medio-lateral (ML) direction, and the Z -axis pointing downward, in the vertical direction. Real-time visual feedback on the AP and ML coordinates of the center of pressure (COP_{AP} and COP_{ML} , respectively) was provided using a 19" monitor positioned at

the eye level about 1.5 m away from the subject. COP_{AP} displacement forward and backward caused cursor motion up and down while COP_{ML} motion caused cursor motion left and right.

A Trigno Wireless System (Delsys, Inc. USA) was used to record surface muscle activity (EMG) of thirteen leg and trunk muscles on the right side of the body: tibialis anterior (TA), soleus (SOL), gastrocnemius medialis (GM), gastrocnemius lateralis (GL), biceps femoris (BF), semitendinosus (ST), vastus lateralis (VL), rectus femoris (RF), vastus medialis (VM), tensor fascia latae (TFL), rectus abdominis (RA), lumbar erector spinae (LES), and thoracic erector spinae (TES). Active electrodes were fixed over the bellies of these muscles using double-sided adhesive tape. EMG signals were amplified and band-pass filtered (20–450 Hz) before being transmitted to a data collection desktop computer (Dell, Core™ i7, 2.93 GHz). EMG and force platform data were collected using a customized LabView program (LabView 2014, National Instruments, Austin, TX, USA) with a sampling frequency of 1 kHz with 16-bit resolution (PCI-6225, National Instruments).

Procedure

Prior to data collection, subjects got familiar with the procedure. Figure 1 demonstrates the experimental setup. Two types of constraints were used in this study, mechanical and visual. The mechanical constraint was varied by asking the subjects to stand barefoot on one of the three specially constructed wooden boards (45×45 cm) with the same height (5.5 cm). These boards had different medio-lateral support size: (1) The stable board (SB) was fully supported by three beams under its surface along the two sides and the midline (Fig. 1A); (2) The wide board (WB) had a 7.6-cm-wide beam under its surface along the midline (Fig. 1B); and (3) The narrow board (NB) had a 3.8-cm-wide beam under the surface along the midline (Fig. 1C). During the experiment, these wooden boards were placed on top of the force plate such that the beams were in the sagittal plane to cause instability in the ML direction. The center of the supporting beam was aligned with the center of the force platform.

We used visual feedback to set permissible deviations of COP_{ML} to serve as a constraint on performance. The visual-feedback-based (visual-FB) constraint was implemented by showing limits for the COP_{ML} deviation on the feedback monitor with vertical target lines. There were three conditions matching the three boards: (1) No visual constraint (CNo); (2) wide constraint (CW) that matched the width of the wide board; and (3) narrow constraint (CN) matching the width of the narrow board. In the CW and CN conditions, subjects were supposed to move in such a way that the cursor did not leave the area restricted by the two vertical lines (Fig. 1 top panel).

Prior to each trial each subject adjusted the upright posture and foot placement to make sure that the COP location was in the middle between the targets shown on the feedback monitor. This point coincided with the center of the force platform.

Each block of trials started with the quiet stance task. Subjects were instructed to stand quietly on one of the boards (with arms crossed over the chest and feet parallel at the shoulder width) and to look at a fixed point on the screen located in front of them for 30 s.

The same foot position, marked on the force plat and boards, was used for all trials across conditions.

The main test consisted of voluntary body sway task in the anterior-posterior (AP) direction for 35 s with two different frequencies: 0.33 Hz (slow) and 0.66 Hz (fast) paced by an auditory metronome. Each trial started with the participant standing quietly. Then, the metronome was turned on, and the participant was asked to begin swaying. During this task subjects were asked to move mainly about ankle joints and keep arms crossed over the chest in a comfortable position. The instruction was to sway continuously in the AP direction between two targets, shown by horizontal lines, while keeping full contact of both feet with the board and to keep COP_{ML} displacements within the vertical target lines. Horizontal target lines were apart 6 cm from each other and had an error margin of 1 cm.

The order of visual and mechanical conditions was block randomized. On the stable board, each participant performed three trials per each of the six condition: two frequencies (slow and fast) $\times$ three visual constraints (SB-CNo, SB-CW, and SB-CN). On each unstable board, participants performed three trials per each of the four conditions: two frequencies (slow and fast) $\times$ two visual constraints (WB-CNo and WB-CW for the wide board, and NB-CNo and NB-CN for the narrow board). There was a 10-s rest period after each trial. After each block of nine trials in the SB conditions and after each block of six trials in the WB and NB conditions, a 5-min break was enforced. In total, each subject performed 42 sway trials and three quiet stance trials. If edges of the unstable board touched the surface of the force platform during a trial, that trial was stopped and repeated. During swaying on the wide board only three trials were repeated across all subjects; one trial for WB-CNo 0.33 Hz, one trial for WB-WC 0.33 Hz, and one trial for WB-WC 0.66 Hz. In the narrow board condition, a total of 22 trials were discarded. Mostly, these happened for the NB-CNo condition at 0.33 Hz (10 trials). In other conditions, the number of discarded trials was within the range from 3 to 5. Given the relatively modest number of discarded trials, we believe that these trials were not a major factor impacting the results and their interpretation.

Data processing

All signals were processed offline using a customized MATLAB R2016a program. The force plate signals were low-pass filtered at 10 Hz with a fourth-order, zero-lag Butterworth filter. Center of pressure (COP) coordinates in AP and ML directions were computed using standard procedures (Winter et al. 1996), considering the height of the boards. For the sway tasks, only the interval (5–34 s) was taken into account to avoid incomplete cycles at the beginning and at the end of each trial. Subjects performed 7 and 15 full cycles for 0.33 Hz and 0.66 Hz trials, respectively. Within each trial, a cycle was defined as the time interval between two successive anterior-most COP_{AP} coordinates. For the computation of muscle modes (M-modes; see below), the sway cycles were time normalized to 100%.

Index of spontaneous postural sway—During quiet stance trials, the root mean square of the COP trajectory was calculated in the medio-lateral (RMS_{ML}) and anterior-posterior (RMS_{AP}) directions over the trial duration.

EMG processing—Raw EMG signals were band-pass filtered (20–360 Hz) using a fourth-order, zero-lag Butterworth filter and rectified. Since we were interested in relatively slow changes in the EMG signals, a moving average 100-ms window was applied. EMG data were shifted 50 ms backward with respect to the force platform data to compensate for the electro-mechanical delay (Corcos et al. 1992). Each EMG signal was corrected for its baseline background activity collected during the quiet stance trials and then normalized to its maximal value seen across all the cycles:

$$IEMG_{NORM} = (IEMG - IEMG_{QS}) / IEMG_{MAX}$$

where $IEMG_{QS}$ is the average of rectified EMG during the quiet stance trial integrated over a 50-ms time window; $IEMG_{MAX}$ is the maximal value of rectified, filtered and averaged over 50 ms time window EMG across all cycles.

Defining M-modes—We defined groups of muscles with parallel scaling of activation levels during the sway task (M-modes) using principal component analysis (PCA) with Varimax rotation and factor extraction (Krishnamoorthy et al. 2003a,b) applied to the correlation matrix of the $IEMG_{NORM}$ data for each condition and each subject. Based on the Kaiser (1960) criterion (eigenvalues > 1), we selected the first four eigenvectors to reduce the 13-dimensional muscle space to a four-dimensional factor (M-mode) space. In addition, we used a criterion that each principal component had to have at least one muscle with absolute value of the loading value > 0.5. We used PCA with rotation and factor extraction rather than non-negative matrix factorization or independent component analysis. Note that we analyzed the differences between integrated EMG signals, which can be both positive and negative; so, the non-negative matrix factorization method would not be appropriate. Besides, further analysis benefits greatly from having an orthogonal system of eigenvectors, which is provided by our method, but not other methods. Note that an earlier study has shown about equally adequate results for the three mentioned methods as long as rotation and factor extraction is used (Tresch et al. 2006). Selecting a fixed number of factors (M-modes) across subjects is also important. Further analysis quantified outcome variables per dimension in the corresponding spaces (see below). This makes analysis within spaces of different dimensionalities questionable because adding or removing an M-mode naturally increases dimensionality of one of the subspaces (UCM) without changing dimensionality of ORT. The amount of variance in the original muscle activation space was computed for each of the M-modes. The magnitudes of the M-modes were calculated multiplying the $IEMG_{NORM}$ in each sway trial by the four eigenvectors.

Defining the Jacobian matrix—Linear relations between small changes in the magnitude of M-mode (ΔM) and the COP_{AP} shifts (ΔCOP_{AP}) were postulated (Krishnamoorthy et al. 2003b; Danna-dos-Santos 2007). The multiple linear regression analysis without intercept was performed over all selected cycles:

$$\Delta COP_{AP} = k_1 \Delta M_1 + k_2 \Delta M_2 + k_3 \Delta M_3 + k_4 \Delta M_4$$

Prior to performing the regression analysis, a low-pass fourth-order, zero-lag Butterworth filter was used to filter $\dot{M}$ and COP_{AP} data at 2 Hz to remove effects of signal fluctuations at frequencies much over the task frequency (0.5 Hz). For each participant and condition,

$\dot{M}$ and COP_{AP} values were computed over all cycles for each 1% of the cycle duration. The coefficients of the multiple linear regression analysis were used as estimates of the Jacobian matrix: $\mathbf{J} = [k_1 \ k_2 \ k_3 \ k_4]$ for each participant and condition separately.

Analysis of inter-cycle variance—The framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999) was used to analyze synergies stabilizing COP_{AP} in the M-mode space. The UCM for COP_{AP} was estimated as the null-space of the $\mathbf{J}$ matrix. The inter-cycle variance in the M-mode space was partitioned into two components, variance parallel to the UCM (V_{UCM}) and orthogonal to the UCM (V_{ORT}). V_{UCM} by definition does not affect the salient performance variable (COP_{AP}), whereas V_{ORT} does.

The M-mode space has dimensionality $n = 4$. The hypothesis that COP_{AP} coordinate is stabilized, accounts for one degree of freedom ($d = 1$), which means that the dimensionality of the UCM is three and of the ORT is one. For each time window, the mean magnitude over the number of cycles of each of the M-modes was calculated ($\overline{\Delta M}$) and was subtracted from the vectors of the individual changes in the magnitudes of the M-mode (ΔM) for each cycle: $\Delta M_{demeaned} = \Delta M - \overline{\Delta M}$.

The residual mean-free vectors $\Delta M_{demeaned}$ were calculated for each condition and for each of the subjects. The UCM was approximated with the null-space of the corresponding $\mathbf{J}$. The null-space of $\mathbf{J}$ is a set of all vector solutions $\mathbf{x}$ of a system of equations $\mathbf{J}\mathbf{x} = 0$; it is spanned by basis vectors, $\mathbf{e}_i$. The vector $\Delta M_{demeaned}$ was resolved into its projection onto the UCM (f_{UCM}) and the orthogonal subspace (f_{ORT}):

$$f_{UCM} = \sum_{i=1}^{n-d} \left(\mathbf{e}_i^T \cdot \Delta M_{demeaned} \right)^T \cdot \mathbf{e}_i^T$$

$$f_{ORT} = \Delta M_{demeaned} - (f_{UCM})^T$$

The trial-to-trial V_{UCM} and V_{ORT} as well as the total variance (V_{TOT}) normalized by the number of DOF of the respective spaces were calculated as:

$$V_{UCM} = \sigma_{UCM}^2 = \frac{1}{(n-d)N_{trials}} \sum_{i=1}^N f_{UCM}^2$$

$$V_{ORT} = \sigma_{ORT}^2 = \frac{1}{dN_{trials}} \sum_{i=1}^N f_{ORT}^2$$

$$V_{TOT} = \sigma_{TOT}^2 = \frac{1}{(d+n)N_{trials}} \sum_{i=1}^N (\Delta M_{demeaned})^2$$

$V_{UCM} > V_{ORT}$ was taken as a sign of a synergy stabilizing COP_{AP} . An index of synergy (V) was calculated to quantify the relative amount of inter-cycle variance that is consistent with stabilizing COP_{AP} coordinates: $V = (V_{UCM} - V_{ORT})/V_{TOT}$, where, V_{TOT} is total variance normalized by dimension ($n=4$). For further statistical analysis, V was log-transformed using Fisher's z-transformation, V_Z (Solnik et al. 2013). This analysis was run for each condition and each subject separately.

Analysis of motor equivalence—The motor equivalence analysis quantified the amount of motion in the M-mode space along the UCM subspace (preserving COP_{AP}) and along the ORT subspace (leading to COP_{AP} changes) across consecutive sway cycles. The former component is addressed as motor equivalent (ME), and the latter as non-motor equivalent (nME). M-mode vectors in the 4D space of M-modes were computed for each 1% epoch of each cycle. Then, the difference between the M-mode vectors at the same phase in consecutive cycles was computed. Finally, we projected the difference vectors onto the UCM and ORT subspaces and computed the length of those projections, normalized by the square root of the corresponding dimensionalities (one and three, respectively; cf. Mattos et al. 2011, 2014) and used as the ME and nME indices. For further statistical analysis, ME and nME component magnitudes were averaged across cycles for each subject and condition separately.

Comparison between inter-cycle variance and motor equivalence—We used two methods to estimate similarity of the outcome indices of the inter-cycle variance analysis (V_{UCM} and V_{ORT} and also $\sqrt{V_{UCM}}$ and $\sqrt{V_{ORT}}$) and motor equivalence analysis (ME and nME). First, we quantified the across-subjects Pearson's correlations between the average values of ME (nME) and V_{UCM} (V_{ORT}) as well as between the average values of ME (nME) and $\sqrt{V_{UCM}}$ ($\sqrt{V_{ORT}}$). For this analysis, each index was averaged over each of the four phases (95–5%, 20–30%, 45–55%, and 70–80%) of the sway cycle, and correlations were computed for each condition, each frequency, and each phase separately.

Statistics

The data are presented in the text and figures as means $\pm$ standard errors. To test Hypothesis 1, we explored possible relations between the indices of variance and indices of motor equivalence using cross-correlation analysis between the time profiles of the variables within the sway cycle. We also explored across-subjects correlations between the indices of variance and indices of motor equivalence; for this analysis, each index was averaged within each of the four phases (95–5%, 20–30%, 45–55%, and 70–80%) of the sway cycle. Further, non-parametric methods were used to compare correlations of ME (nME) with V_{UCM} (V_{ORT}) and with $\sqrt{V_{UCM}}$ ($\sqrt{V_{ORT}}$).

To test Hypothesis 2, one-way and two-way repeated-measures ANOVAs were performed to evaluate the effects of *Board* (SB, WB, and NB) and *Visual-FB* (CNo, CW, and CN) on the outcome variables. To test Hypothesis 3, an ANOVA with repeated measures (three factors: *Visual-FB* $\times$ *Component* $\times$ *Frequency*) was used. In particular, we analyzed these effects on the characteristics of sway performance such as COP range in the medio-lateral direction, amount of variance accounted for by the four selected M-modes, indices of inter-cycle variance (V_{UCM} and V_{ORT}), log-transformed index of synergy (V_Z), and indices of motor equivalence (ME and nME). Significant effects were further explored using pairwise contrasts with Bonferroni corrections. The data were tested for normality and sphericity. Geenhouse–Geisser corrections were used to adjust the degrees-of-freedom when necessary. The level of significance was set at $p = 0.05$.

Results

Performance characteristics

Voluntary sway—During voluntary sway tasks in the AP direction performed while standing on the stable board (SB) the subjects showed relatively small COP deviations in the uninstructed direction (COP_{ML}). The average magnitude of these deviations increased significantly with the sway frequency, on average from 1.62 to 2.08 cm for the slow and fast frequencies, respectively ($F_{(1, 22)} = 10.6$; $p < 0.01$). Typical time profiles of COP_{AP} and COP_{ML} are shown in the top panels of Figure 2; note the sine-like, large-amplitude COP_{AP} trajectories and small COP_{ML} deviations. Adding a visual constraint to this task did not show significant effects on the COP_{ML} deviations ($F_{(2, 44)} = 1.03$; $p > 0.3$). Averaged across subjects peak-to-peak COP_{ML} deviations are shown in panel A of Figure 3.

When the subjects performed the sway task while standing on boards with reduced support area, WB and NB, peak-to-peak changes in COP_{ML} showed larger values for NB as compared to WB and SB ($F_{(2, 44)} = 23.5$; $p < 0.001$). Pairwise contrasts confirmed the significant differences between NB and both SB and WB ($p < 0.01$). Significant effects of sway frequency were seen during the performance on SB and WB, but these effects disappeared on the NB; however, the *Board* $\times$ *Frequency* interaction was just under the significance level ($F_{(2, 44)} = 2.97$; $p = 0.06$).

Changing the visual-FB constraints when subjects performed the sway task on an unstable board showed significant effects of *Board* ($F_{(1, 22)} = 30.9$; $p < 0.001$) and *Visual-FB* ($F_{(1, 22)} = 19.9$; $p < 0.001$) on the COP_{ML} deviations. During this analysis, data for the two boards, WB and NB, were compared in the no-constraint condition (CNo) and matched constraint conditions, CW-WB and CN-NB. Visual-FB constraint had no significant effect on COP_{ML} when the voluntary sway task was performed while standing on WB (on average, 1.8 cm). In contrast, there was a significant increase in COP_{ML} deviations when the subjects performed the task under NB-CN (2.79 ± 0.9 cm) compared to WB-CW (1.85 ± 0.5 cm) (*Board* $\times$ *Visual-FB* interaction, $F_{(1, 22)} = 26.3$; $p < 0.001$).

Postural sway during quiet stance—We used the root mean square (RMS) of COP_{AP} and COP_{ML} as an index of postural sway estimated during the 30-s intervals of quiet standing trials. Figure 4 illustrates the RMS in the AP and ML directions. Overall, sway

increased when the subjects stood on boards with narrow support: RMS was larger on WB as compared to SB; it became even larger on NB ($F_{(2, 44)} = 20.9$; $p < 0.001$). RMS_{AP} was larger than RMS_{ML} for the SB and WB conditions, but not for NB (effect of *Direction*, $F_{(1, 22)} = 25.1$; $p < 0.001$ and *Direction* $\times$ *Board* interaction, $F_{(2, 44)} = 6.6$; $p < 0.005$). Pairwise contrasts showed significant differences between SB vs. NB ($p < 0.001$) and WB vs. NB ($p < 0.001$) for RMS_{ML} . Pairwise contrasts for RMS_{AP} showed no significant differences.

Muscle modes and the Jacobian

In the PCA applied to integrated muscle activation indices (see Methods), the first four PCs explained, on average, $75.39 \pm 0.81\%$ of $IEMG_{NORM}$ variance during the slow frequency (0.33 Hz) trials and $74.85 \pm 0.8\%$ of variance in the fast frequency (0.66 Hz) trials. There were no effects of any of the main factors (*Board*, *Visual-FB*, and *Frequency*) on the amount of variance, which ranged from 73.56% to 77.58%.

Table 1 presents the muscle loading factors for the four factors (M-modes) for a representative subject who performed the voluntary sway task in the SB-CNo condition. Significant loading values are shown in bold. There were only minor changes in the pattern of loading values across conditions, more commonly in M3 and M4 modes. Figure 5 illustrates the loading values for all the muscles for the three boards for sway at 0.66 Hz, averaged over the constraint conditions. Note the consistent patterns of muscle loadings for the dorsal and ventral muscles.

M-mode magnitudes showed consistent modulation over the sway cycle. Averaged across subjects profiles of the four M-modes are shown in Figure 6 for both sway frequencies for the SB-CNo condition.

Analysis of inter-cycle variance

Analysis of the two components of the inter-cycle variance (V_{UCM} and V_{ORT} , see Methods) performed in the M-mode space showed qualitatively different profiles for V_{ORT} and V_{UCM} consistent across subjects and conditions. Figure 7A illustrates these profiles averaged across subjects for sway performed at the two frequencies while standing on the SB, without visual-FB constraints (SB-CNo). Note the double-peaked V_{ORT} , with the peaks about 25% and 75% of the sway cycle, and a single peak of V_{UCM} close to the middle of the cycle. Noticeable double-peak V_{ORT} pattern was not clearly seen during WB_CNo in 7 of 12 subjects, during WB_CW in 6 of 12 subjects, and during NB_CN in 7 of 12 subjects for the sway at 0.33 Hz only. When the pair of variance indices were reduced to a single synergy index (V , see Methods), V showed a peak close to the mid-point of the cycle (defined as the most backward COP_{AP} coordinate) and valleys close to 25% and 75% of the cycle (Figure 7B).

When the subjects stood on boards with different support dimension (SB, WB, and NB) without visual constraints, averaged over the sway cycle variance components, V_{UCM} and V_{ORT} , were higher in the NB condition compared to the WB and SB conditions (Figure 8A). This was confirmed by a significant main effect of *Board* ($F_{(2, 88)} = 10.2$, $p < 0.001$) in the three-way ANOVA *Board* (SB-CNo, WB-CNo, NB-CNo) $\times$ *Component* (V_{UCM} and V_{ORT})

$\times$ *Frequency* (slow and fast). The effect of *Component* was just under the significance level ($p = 0.059$). Pairwise contrasts indicated significantly higher variance indices for NB compared to SB ($p < 0.01$) and WB board ($p < 0.001$). The increase in V_{UCM} and V_{ORT} was not accompanied by a change in the synergy index V .

In contrast, there were no significant effects of visual-FB constraint on the variance components. The three-way ANOVA, *Visual-FB* (SB-CNo, SB-WC, and SB-NC) $\times$ *Component* $\times$ *Frequency* for the data during standing on the stable board (SB), showed only a significant main effect of *Component* ($F_{(1, 44)} = 7.02$, $p < 0.01$) reflecting larger V_{ORT} as compared to V_{UCM} , without other main effects and without interactions. Similarly, no effects of visual-FB constraints were found during standing on WB and NB, and there were no interactions between *Visual-FB* and other factors.

Analysis of motor equivalence

Analysis of motor equivalence revealed profiles of the two components of cycle-to-cycle changes in the M-mode space, ME and nME, that were similar to the aforementioned patterns of V_{UCM} and V_{ORT} . In particular, nME showed two peaks close to 25% and 75% of the sway cycle, while ME had a tendency to show a single peak about the middle of the cycle (see Fig. 9)

Effects of mechanical constraints on the ME and nME indices were similar to the described effects on V_{UCM} and V_{ORT} (Figure 8B). In particular, both ME and nME increased when the task was performed while standing on the NB ($F_{(2, 88)} = 8.05$, $p < 0.001$) and overall $nME > ME$ (0.159 ± 0.003 vs 0.128 ± 0.003 ; $F_{(1, 44)} = 54.3$; $p < 0.001$). Both ME and nME magnitudes were smaller during swaying at the high frequency compared to the slow frequency (0.132 ± 0.004 vs 0.171 ± 0.004 ; $F_{(1, 44)} = 15.3$; $p < 0.001$).

There were no significant effects of visual constraints on the ME and nME components. A three-way ANOVA, *Visual-FB* (SB-CNo, SB-WC and SB-NC) $\times$ *Component* (ME and nME) $\times$ *Frequency* on the data while standing on the SB, showed only a significant main effect of *Component* ($F_{(1, 44)} = 7.59$, $p < 0.01$) without other significant effects and interactions. Similar results (effects of *Component* only; $p < 0.01$) were seen in ANOVAs on the data while standing on the WB and NB.

Comparison between inter-cycle variance and motor equivalence analyses

Pearson correlations between the average values of ME (nME) and V_{UCM} (V_{ORT}) as well as between the average values of ME (nME) and $\sqrt{V_{UCM}}(\sqrt{V_{ORT}})$ were computed for each condition, each frequency, and each phase separately. Overall, during the faster sway (0.66 Hz), the number of significant correlations was 106 (out of 112), while during the slower sway (0.33 Hz), the number of significant correlations was 68 (out of 112). The median values with the first and third quartiles (quart) of the correlation coefficients were:

ME vs. V_{UCM} : $R = 0.77$, quart 0.685–0.823 for 0.66 Hz and

$R = 0.45$, quart 0.228–0.625 for 0.33 Hz;

ME vs. $\sqrt{V_{UCM}}$: $R = 0.80$, quart 0.718–0.853 for 0.66 Hz and

$R = 0.485$, quart 0.338–0.663 for 0.33 Hz;

nME vs. V_{ORT} : $R = 0.77$, quart 0.728–0.85 for 0.66 Hz and

$R = 0.63$, quart 0.438–0.753 for 0.33 Hz;

nME vs. $\sqrt{V_{ORT}}$: $R = 0.815$, quart 0.78–0.865 for 0.66 Hz and

$R = 0.685$, quart 0.54–0.803 for 0.33 Hz.

Correlation coefficients between the ME (nME) indices and square roots of the variance indices, $\sqrt{V_{UCM}}(\sqrt{V_{ORT}})$ were significantly larger than the correlations between ME (nME) and variance indices, $V_{UCM}(V_{ORT})$. This was confirmed with the sign test: Overall, this was true for 97 (out of 112) comparisons with five ties ($p < 0.01$).

Second, we ran cross-correlation analysis between the corresponding time series for each subject and each condition separately. This analysis was run only for the $\sqrt{V_{UCM}}(\sqrt{V_{ORT}})$ variables given their closer correlation with ME (nME) in the first analysis. Results of the second analysis are shown in Table 2 for each condition and sway frequency separately. Note the overall high magnitudes of the peak of the cross-correlation function, in particular for the analysis of $\sqrt{V_{ORT}}$ vs. nME at the high sway frequency (0.66 Hz), see also Figure 10. Each of the values is significant at $p < 0.05$. Note also the small time delays of the peak value of the cross-correlation function, on average, 0.002 ± 0.08 s.

Discussion

Most of the specific hypotheses formulated in the Introduction have been disproven. The notable exception is the first hypothesis predicting correlation between the outcome variables of the two types of analysis, inter-cycle variance analysis and analysis of motor equivalence. Indeed, we observed significant correlations between V_{UCM} and ME and between V_{ORT} and nME. By itself, this is an important result (although not unexpected, see later), which allows using either one of the methods to produce quantitative indices of synergies stabilizing salient performance variables. This is potentially important for studies of populations with impaired motor abilities who may be able to perform only a few consistent trials at a given task, which may be sufficient for the ME analysis but not for variance analysis.

Other specific hypotheses were falsified. Indeed, we expected significant effects of both mechanical and visual constraints on multi-mode synergies stabilizing the COP_{AP} trajectory (Hypothesis 2). While mechanical constraints affected indices of performance, such as deviations of COP in the uninstructed direction (COP_{ML}) and indices of postural sway, these constraints had no consistent effect on the amount of variance accounted for by the selected four M-modes, indices of inter-cycle variance, and indices of motor equivalence. Visual constraints had smaller effects on performance and were equally ineffective in changing most outcomes of the synergy analyses. In fact, ME analysis showed stronger effects of

visual constraints than of mechanical constraints in contradiction to Hypothesis 2B. So, synergy metrics showed their robustness across conditions with additional constraints, which were effective in changing indices of performance. Our exploration of the effects of sway speed (Hypothesis 3) also led to unexpected results. In particular, we observed a drop in ME with sway speed (opposite to the expected changes) in the absence of significant effects on other outcome metrics.

Further we discuss implication of the current results for the concept of multi-muscle synergies ensuring stability of whole-body actions and for the scheme with two types of control variables, those that define patterns of salient performance variables and those that define stability properties of those performance variables.

Synergies in the general scheme of postural control

Our study has been designed and performed within the physical view on the neural control of movements (reviewed in Latash 2016, 2017). A major alternative approach to the problem of postural control in the field of gravity has been based on the control theory coupled with the idea of stabilizing an inverted pendulum (Winter et al. 1996). In particular, such schemes analyze the role of different sensory feedback loops in the control of vertical posture (Maurer et al. 2006; Goodworth and Peterka 2012). This approach led to the idea of sensory re-weighting based on changes in external constraints, state of the body, and relevant experience (Horak et al. 1994; Assländer and Peterka 2016). While we appreciate the progress achieved using this approach, in our opinion if one wants to discover laws of nature that produce biological movement (and posture), a physical approach to biological movement has to be developed.

According to the physical view, the body, including the central nervous system, is a physical system that behaves according to laws of nature and performs no computations. The neural control of actions involves generating time patterns of parameters of physical laws that define interactions among structures within the body and between the body and the environment. According to the idea of control with referent coordinates (RC; reviewed in Feldman 2015), any task starts with specifying time profiles of a relatively low-dimensional set of spatial RCs for salient variables. Further, a sequence of few-to-many transformations leads to RCs at hierarchically lower levels such as those that define involvement of individual limbs, digits, joints, and muscles. According to the principle of abundance (Gelfand and Latash 1998; Latash 2012), these transformations are organized in a synergic way, i.e., they do not produce single, optimal solutions but allow freedom of changes in RCs at hierarchically lower levels as long as these changes are compatible with the task-specific RC defined at the task level.

This general idea has been formalized within the UCM hypothesis framework, which introduced a method of quantifying inter-trial (inter-cycle) structure of variance (Scholz and Schöner 1999). This method has been mostly used for variance analysis in spaces of elemental variables defined as performance variables produced by individual elements involved in task performance (such as joint rotations, digit forces, muscle group activations, etc.). Only recently, this method has been applied to analysis at the level of hidden, control variables (RC, Ambike et al. 2015, 2016), which are much harder to quantify objectively. In

our study, we also used this method, as well as the complementary method of analysis of motor equivalence (Scholz et al. 2007, 2011; Mattos et al. 2013), at the level of muscle activation variables considered as elemental variables. Note that we do not assume that muscle activations (or M-modes computed from muscle activation) are in any way prescribed by the central nervous system. Within the current theoretical scheme, M-modes are consequences of shifts of whole-body elementary RCs, which may be viewed as the control basis (related to the notion of primitives, Kargo et al. 2010; Dominici et al. 2011; Bizzi and Cheung 2013) for building synergies stabilizing important mechanical variables such as COP coordinates.

The notion of *synergy* has been used in the movement literature in different meanings. In particular, the notion of pathological synergies has been used to describe stereotypical patterns of muscle activation and joint involvement that interfere with purposeful movements in certain groups of patients such as stroke survivors (DeWald et al. 1995). More frequently, synergy means a group of variables (kinetic, kinematic, or electromyographic) that show parallel changes with task parameters and/or over the time of action (d'Avella et al. 2003; Ivanenko et al. 2004; Ting and Macpherson 2005; Tresch et al. 2006). We use this word for neural organizations that provide stability of salient performance variables (reviewed in Latash 2008). So, to avoid confusion, we refer to groups of elements (muscles) that show parallel changes in their output variables (EMG) as M-modes (Krishnamoorthy et al. 2003a).

Neural mechanisms of synergies are unknown. Several schemes have been suggested that range from optimal feedback control schemes (Todorov and Jordan 2002) to schemes with back-coupling from peripheral receptors and within the central nervous system (Latash et al. 2005; Martin et al. 2009). Within the latter schemes, two types of neural variables are specified to produce an action. One of these groups (NV1) define characteristics of the action seen in averaged across trials patterns, while the other group (NV2) defines stability properties of those variables and is reflected in such indices as variance structure (relative amounts of V_{UCM} and V_{ORT}) and motor equivalence (ME vs. nME). Note that synergies are not obligatory for task performance. For example, young, healthy persons may show no synergies stabilizing a performance variable, even though it has been explicitly instructed by the task (Latash et al. 2001). The existence of NV1 and NV2 has been indirectly supported by observations of changes in synergy indices without a change in the performance (Olafsdottir et al. 2005; Shim et al. 2005, 2007).

Some of our results support the scheme with two groups of neural variables. In particular, manipulations of mechanical and visual constraints showed significant effects on such performance variables as COP_{ML} deviations and characteristics of postural sway supposedly reflecting NV1. In contrast, there were no effects on any synergy indices, supposedly defined by NV2.

The increase in the sway magnitude during quiet standing in more challenging conditions confirms results of earlier studies (Mochizuki et al. 2006) that were used to argue in favor of the theory that sway is not a reflection of “neural noise” but a purposeful process, possibly reflecting search for limits of stability (Riccio 1993). This view is compatible with results of

the rambling-trembling sway decomposition (Zatsiorsky and Duarte 1999) suggesting superposition of two processes reflecting changes in the body RC (rambling) and properties of peripheral apparatus including reflexes (trembling).

Motor equivalence and structure of variance

While the two indices of motor synergies developed within the UCM hypothesis have been known for about 10 years (Krishnamoorthy et al. 2003b; Scholz et al. 2007), there have been only a few direct comparisons of the two methods of analysis. In particular, Mattos and her colleagues (Mattos et al. 2011, 2015) have shown different statistical behaviors of the indices reflecting variance structure (V_{UCM} and V_{ORT}) and those reflecting the use of motor equivalent actions (ME and nME). This was shown in series of both discrete arm movements and cyclical multi-finger tasks. Note that in cyclical tasks, analyses of inter-cycle variance (as in the analysis of V_{UCM} and V_{ORT}) and inter-cycle mean distances (as in the analysis of ME and nME motions) are linked for normally distributed data.

Indeed, assume that each measurement at a particular phase of the cycle represents a sample from a normal distribution with the standard deviation σ . Then, the difference between two random samples will also be normally distributed with the mean $\mu = 0$ and standard deviation, $\sigma_D = \sigma\sqrt{2}$. Since ME analysis involves the computation of absolute distances between data points in consecutive cycles, the distribution of those distances is non-negative (folded) with a new mean (μ_X) and new standard deviation (σ_X) (Leone et al. 1961):

$$\mu_X = \sigma\sqrt{2/\pi}$$

$$\sigma_X^2 = \sigma^2 - \mu_X^2$$

These equations can be applied to data within the UCM to produce ME and within ORT to produce nME. They suggest, that $\sqrt{V_{UCM}}$ should correlate with ME and $\sqrt{V_{ORT}}$ should correlate with nME (see Hypothesis 1 in the Introduction). Correlations with squared magnitudes of standard deviations, V_{UCM} and V_{ORT} , also are expected, although they may be weaker.

Our results confirm these predictions. In particular, we observed stronger correlations between the ME (nME) indices and square roots from the variance indices, $\sqrt{V_{UCM}}$ ($\sqrt{V_{ORT}}$), as compared to the correlations with the variance indices themselves, V_{UCM} (V_{ORT}). Why did the cited earlier studies found different statistical effects on metrics of variance analysis and motor equivalence analysis? There may be a few reasons. First, Eqs (1) are expected only for data with perfectly normal distributions. So, deviations from normality might lead to different statistical behaviors of $\sqrt{V_{UCM}}$ and $\sqrt{V_{ORT}}$ as compared to ME and nME. The second reason is that indices of variance might show statistically different effects compared to indices of standard deviation.

While the two sets of indices, those of inter-trial variance and of motor equivalence, reflected the same property of the system, i.e., its stability, they both have advantages and disadvantages. Estimating variance across trials within the UCM and ORT spaces requires multiple trials by definition. The number of trials is undefined but so far no studies, to our knowledge, used fewer than 10 trials to estimate structure of inter-trial variance (the lowest example we are aware of is 12 trials in Scholz et al. 2004) and most studies used 20 trials (or cycles, as in the current study). ME and nME are indices of motion in the same spaces, UCM and ORT, that can be quantified in a single trial. Of course, averaging these indices over a few trials has the advantage of providing more reliable estimates and avoiding spurious results. So far, no estimates of ME/nME reliability with a change in the number of trials have been available.

Being able to measure the main outcome indices in single trials is a clear advantage of ME/nME, in particular in special populations. On the other hand, inter-trial variance indices have been used for many years in numerous studies (reviewed in Latash 2008; Latash and Zatsiorsky 2016) and, as a result, may be viewed as reliable synergy indices sensitive to aging, neurological disorder, atypical development, and exercise. ME and nME have been used so far only in a handful of studies; we do not know whether they are as reliable and sensitive as the variance indices are. This gives the variance indices an advantage. Sensitivity of ME/nME across tasks, conditions, and populations has to be explored to mitigate the latter factor. In the current study, we used all the available cycles to get most reliable estimates of both inter-cycle variance indices and indices of motor equivalence. We plan to explore changes in both indices with the number of trials in future.

We discovered no effects of sway frequency on any of the metrics reflecting multi-muscle synergies. One of the earlier studies (Danna-dos-Santos et al. 2007) explored indices of M-mode variance within a very broad range of sway frequencies and reported parallel increase in V_{UCM} and V_{ORT} with no change in the synergy index V with sway frequency. Our inability to detect similar differences between the slow and fast conditions might be due to the fact that we explored a relatively narrow range of frequencies as compared to the mentioned earlier study.

A study of multi-joint reaching movements performed at different velocities (Scholz et al. 2011) discovered large ME components of motion within the joint configuration space, and both the ME and nME motion increased with movement speed. In contrast, in our experiment, both ME and nME magnitudes were larger during sway at the slow frequency compared to the fast frequency, i.e., they dropped with movement speed. It is possible that the nature of different tasks, discrete vs. cyclical, was the main reason for the difference in the findings. An earlier study explored the effects of speed on the V_{UCM} and V_{ORT} components during discrete and cyclical multi-finger actions (Friedman et al. 2009). The effects were dramatically different. In particular, there were strong effects of movement speed on V_{ORT} during discrete actions (expected from earlier studies and a model, Latash et al. 2002; Goodman et al. 2005) but not during cyclical actions. Those observations provided support for the idea of different control processes underlying discrete and cyclical actions (Sternad and Dean 2003; Hogan and Sternad 2007).

Mechanical and visual-feedback-based constraints in postural tasks

Maintenance of vertical posture in the field of gravity gets contributions from sensory signals of different modalities including visual, vestibular, and somatosensory signals (reviewed in Mergner 2010). Visual information is one of the most important sources of information for postural control and under conditions of altered information from other sensory sources, subjects are able to keep vertical posture as long as vision is available. The importance of visual feedback has been demonstrated, in particular, using the ‘moving room paradigm’ when the visual surround is manipulated either by actually moving the room or by altering the display in front of the subject that mimics motion of the visual surround (Dijkstra et al. 1994). For example, when the visual surround accelerates towards the subject, an actual backward sway of the body is observed.

Manipulating vision-based constraints can lead to unexpected consequences for motor performance. In most motor tasks, presenting a smaller target for a salient performance variable leads to a decrease in variability of that variable, sometimes at the expense of movement speed as in the classical Fitts’ Law (Fitts 1954). In contrast, when a standing person is asked to reduce natural postural sway and provided with a visual target and veridical feedback on the COP migration, an increase in the sway is observed rather than its attenuation (Danna-dos-Santos et al. 2008). The specificity of the control of whole-body tasks is also reflected in deviations of the dependence of movement time on distance and target size from the Fitts’ Law (Danion et al. 1999; Duarte and Freitas 2005).

When visual information is unavailable, e.g., when a person stands with eyes closed, sensory signals of other modalities become highly important. Earlier in the XX-th century, untreated syphilis could lead to a state called *tabes dorsalis*, characterized by disrupted transmission of sensory signals along the dorsal columns of the spinal cord. Those patients could only stand with their eyes open. Similar observations have been made in patients with peripheral sensory problems caused by advanced stages of diabetes and by large-fiber peripheral neuropathy (Sanes et al. 1985; van Deursen and Simoneau 1999). The importance of proprioceptive information is also demonstrated by so-called vibration-induced fallings during the application of high-frequency, low-amplitude muscle vibration to leg muscles (Eklund and Hagbarth 1967; Roll and Vedel 1980).

Manipulating mechanical constraints can also lead to counter-intuitive consequences. For example, standing on a surface with reduced support area is characterized by increased indices of spontaneous postural sway (Mochizuki et al. 2006), which is clearly detrimental for performance and could even lead to failure at the task.

Interactions between mechanical and sensory constraints have also been documented. For example, light touch (a sensory cue with minimal mechanical effect) is known to lead to a decrease in the spontaneous postural sway (Jeka and Lackner 1994). It also leads to changes in anticipatory postural adjustments (APAs, Belenkiy et al. 1967; reviewed in Massion 1992) seen prior to a self-inflicted perturbation when subjects stand on stable and unstable boards (Slijper and Latash 2000). In our experiment, visual constraints had no effect on performance when the subjects stood on the stable board (SB), but these effects became significant during standing on the CN board.

The aforementioned interpretation of the results in terms of effects on only one group of hypothetical neural variables, NV1, not NV2, allows speculating about the involvement of different neurophysiological structures in the observed effects. A series of recent studies have documented very strong effects of neurological disorders affecting subcortical structures, such as the cerebellum and basal ganglia, on indices of synergies (Park et al. 2012, 2013; Latash and Huang 2015; Falaki et al. 2016). This has been shown in early-stage Parkinson's disease (Park et al. 2012) and even in healthy persons at high risk of parkinsonism (Lewis et al. 2016). In contrast, mild cortical stroke leads to significant impairment of motor performance with only mild and frequently non-significant changes in synergy indices, such as ΣV (Reisman and Scholz 2003; Jo et al. 2016). Of course, separation of disorders into cortical and subcortical should be taken with a grain of salt given that loops link all those structures. Nevertheless, significant effects of constraints in our study on performance indices but not on synergy indices suggest that varying constraints affects selection of NV1, while NV2 remain relatively unaffected.

Concluding comments

We would like to end by emphasizing two important results of our study. First, the manipulation of mechanical and visual constraints had significant effects on performance indices but not on synergy indices. This result shows that the neural control of performance and of its stability may involve different control variables and neurophysiological structures. Second, the two methods of analysis of multi-muscle synergies, analysis of inter-cycle variance and analysis of motor equivalence, led to correlated outcome indices. Such correlations could be expected from statistical considerations under particular assumptions, but they were not obvious upfront. This result has potential importance for studies of patients with movement disorders who may be unable to perform multiple trials (cycles) at a given task making variance analysis questionable. In such patients, analysis of motor equivalence may present a viable alternative because the ME and nME indices can be computed within a single trial.

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Figure 1.

An illustration of the experimental setup. The subject was standing on one of the three boards: SB - stable board, WB - wide board, or NB - narrow board. Visual feedback showed two targets for the anterior-posterior shifts of the center of pressure, COP_{AP} . The screen could show no constraints for the medio-lateral COP displacement (CNo), constraints matched to the wide board (CW) or to the narrow board (CN). EMGs were recorded from the right side of the body: TA - tibialis anterior, SOL - soleus, GM - gastrocnemius medialis, GL - gastrocnemius lateralis, BF - biceps femoris, ST - semitendinosus, VL - vastus lateralis, RF - rectus femoris, VM - vastus medialis, TFL - tensor fascia lata, RA - rectus abdominis, LES - lumbar erector spinae, TES - thoracic erector spinae.

Figure 2.

Typical time profiles of COP_{AP} and COP_{ML} (the top panels) and $IEMG_{NORM}$ (the middle and bottom panels) for a representative subject for the two frequencies of sway: slow (0.33 Hz) - left column and fast (0.66 Hz) - right column. The sway duration is normalized to 100%. TA - tibialis anterior, SOL - soleus RF - rectus femoris and ST - semitendinosus. AP - anterior-posterior, ML - medio-lateral, F - forward, B - backward.

Figure 3.

Peak-to-peak COP_{ML} deviations (means with standard error bars) **A** - stable board conditions with different feedback; **B** - different boards. SB - stable board, WB - wide board, NB - narrow board, CNo - no constraint, CW - wide constraint, CN - narrow constraint, * - statistical significance ($p < 0.05$).

Figure 4. RMS of COP deviations in the anterior-posterior (AP) and medio-lateral (ML) directions (mean across subjects with standard error bars) during the quiet standing trials. SB - stable board, WB - wide board, NB - narrow board, * - statistical significance ($p < 0.05$).

Figure 5.

Loading values for the first two M-modes (M1 – black bars; M2 – light, striped bars) averaged across subjects and visual-FB conditions for the 0.66 frequency sway are shown with standard error bars for the three boards separately. A: stable board (SB), B: wide board (WB), C: narrow board (NB). Tibialis anterior - TA, soleus - SOL, gastrocnemius medialis - GM, gastrocnemius lateralis - GL, biceps femoris - BF, semitendinosus - ST, vastus lateralis - VL, rectus femoris - RF, vastus medialis - VM, tensor fascia lata - TFL, rectus abdominis - RA, lumbar erector spinae - LES, thoracic erector spinae - TES.

Figure 6.

The time profiles of muscle modes (M-modes) for the slow (0.33 Hz - left panel) and fast (0.66 Hz - right panel) sway conditions. Mean data across subjects are shown with standard error shades for standing on the stable board without any constraint (SB-CNo).

Figure 7.

A: The inter-cycles variance components, V_{UCM} - solid line and V_{ORT} - dashed line, for the slow (0.33 Hz - left panel) and fast (0.66 Hz - right panel) sway. Note the characteristic double-peak shape of V_{ORT} and single-peak shape of V_{UCM} . B: The synergy index (ΔV_Z) for the slow (0.33 Hz) - left panel and fast (0.66 Hz) - right panel sway. F - forward, B - backward. Averaged across subjects values with standard error shades are shown for the SB-CNo (stable board, no visual constraint) condition.

Figure 8.

A: The two components of the inter-cycle variance (V_{UCM} and V_{ORT}) for the different board without visual constraints. B: The ME and nME indices for the different boards without visual constraints. SB - stable board, WB - wide board, NB - narrow board, CNo - no visual constraint. * - statistical significance ($p < 0.05$).

Figure 9.

Two components of the cycle-to-cycle motion in the M-mode space: motor equivalent (ME, solid line) and non-motor equivalence (nME, dashed line) for the slow (0.33 Hz, left panel) and fast (0.66 Hz, right panel) sway. Means across subject with standard error shades are shown for the stable board condition with no constraint (SB-NCo).

Figure 10.

The cross-correlation functions, $\sqrt{V_{ORT}}$ vs. nME for the sway at high (0.66 Hz, the blue line) and slow frequency (0.33 Hz, black line). The data are for a typical subject (SUB_01) for the SB-CNo (stable board, no visual constraint) condition.

Table 1.

Typical loading factors for the PCA

Frequency	0.33 Hz				0.66 Hz			
Muscle	M1	M2	M3	M4	M1	M2	M3	M4
TA	0.16	-0.02	-0.04	0.98	0.02	0.78	-0.06	-0.03
SOL	0.85	-0.21	-0.01	0.10	0.86	-0.25	0.00	0.01
GM	0.93	-0.03	-0.03	0.02	0.90	-0.01	0.03	0.06
GL	0.81	-0.09	-0.06	0.04	0.88	-0.09	-0.07	0.00
BF	0.91	-0.01	-0.01	0.10	0.80	-0.01	0.08	-0.11
ST	0.88	-0.01	-0.03	0.05	0.89	0.02	-0.07	-0.06
VL	-0.07	0.88	0.01	0.00	-0.11	0.90	0.07	0.13
RF	-0.07	0.88	0.00	0.02	-0.08	0.92	0.02	0.13
VM	0.05	0.77	0.04	-0.08	-0.09	0.90	0.05	0.06
TFL	-0.22	0.61	0.00	0.03	-0.16	0.19	0.02	0.95
RA	-0.05	0.04	1.00	-0.04	-0.09	0.03	0.99	0.02
LES	0.88	-0.08	0.01	0.08	0.87	-0.04	-0.11	-0.13
TES	0.81	-0.12	0.00	0.00	0.78	-0.06	-0.12	-0.21

Typical principal component (PC) loadings are shown for the 0.33 Hz and 0.66 Hz sway performed by a representative subject (SUB_01 in SB-CNo). M1, M2, M3, and M4 are the four M-modes. The significant loadings (absolute magnitude over 0.5) are in bold. Tibialis anterior - TA, soleus - SOL, gastrocnemius medialis - GM, gastrocnemius lateralis - GL, biceps femoris - BF, semitendinosus - ST, vastus lateralis - VL, rectus femoris - RF, vastus medialis - VM, tensor fascia lata - TFL, rectus abdominis - RA, lumbar erector spinae - LES, thoracic erector spinae - TES.

Table 2.

Results of the cross-correlation analysis between variance and motor equivalence indices

Condition	Peak R-value			
	$\sqrt{V_{UCM}}$ vs ME		$\sqrt{V_{ORT}}$ vs nME	
	0.33 Hz	0.66 Hz	0.33 Hz	0.66 Hz
SB_CNo	69.66	60.95	46.84	90.51
SB_CW	85.87	87.34	50.94	92.32
SB_CN	65.61	70.88	57.27	81.20
WB_CNo	56.63	71.64	84.95	94.57
WB_CW	75.35	70.74	88.24	90.80
NB_CNo	82.21	65.16	82.10	92.72
NB_CN	76.50	64.57	78.26	95.71

Average across subjects values are presented. SB - stable board, WB - wide board, NB - narrow board, CNo – no constraint, CW – wide constraint, CN – narrow constraint, ME - motor equivalence, nME - non-motor equivalence, $\sqrt{V_{UCM}}$ - square root of variance within the UCM, $\sqrt{V_{ORT}}$ - square root of variance ORT.