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Stability of vertical posture explored with unexpected mechanical perturbations: Synergy indices and motor equivalence

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Abstract

We explored the relations between indices of mechanical stability of vertical posture and synergy indices under unexpected perturbations. The main hypotheses predicted higher posture-stabilizing synergy indices and higher mechanical indices of center of pressure stability during perturbations perceived by subjects as less challenging. Healthy subjects stood on a force platform and held in fully extended arms a bar attached to two loads acting downward and upward. One of the loads was unexpectedly released by the experimenter causing a postural perturbations. In different series, subjects either knew or did not know which of the two loads would be released. Forward perturbations were perceived as more challenging and accompanied by co-activation patterns among the main agonist-antagonist pairs. Backward perturbation led to reciprocal muscle activation patterns and were accompanied by indices of mechanical stability and of posture-stabilizing synergy indicated higher stability. Changes in synergy indices were observed as early as 50-100 ms following the perturbation reflecting involuntary mechanisms. In contrast, predictability of perturbation direction had weak or no effect on mechanical and synergy indices of stability. These observations are interpreted within a hierarchical scheme of synergic control of motor tasks and a hypothesis on the control of movements with shifts of referent coordinates. The findings show direct correspondence between stability indices based on mechanics and on the analysis of multi-muscle synergies. They suggest that involuntary posture-stabilizing mechanisms show synergic organization. They also show that predictability of perturbation direction has strong effects on anticipatory postural adjustment but not corrective adjustments. We offer an interpretation of co-activation patterns that questions their contribution to postural stability.

Keywords

Vertical posture; stability; muscle mode; motor equivalence; synergy

Introduction

Bipedal vertical posture is inherently unstable in the gravity field. Numerous studies have addressed the problem of postural stability from a variety of perspectives including biomechanics, control theory, and physiological mechanisms (reviewed in Nashner et al. 1989; Winter et al. 1999; Maurer et al. 2006; Mergner 2007). Recently, this problem has been addressed within the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999). According to the UCM hypothesis, the central nervous system (CNS) acts in an abundant space of elemental variables (cf. Latash 2012) and organizes in that space a subspace (UCM) corresponding to a stable value of a salient performance variable. This organization leads to a specific structure of inter-trial variance and the phenomenon of motor equivalence. The former is reflected in larger amounts of variance within the UCM as compared to variance in the orthogonal to the UCM space, $V_{\text{UCM}} > V_{\text{ORT}}$ (reviewed in Latash et al. 2007). The latter leads to large displacements within the UCM (motor equivalent, ME) during quick actions while displacements in the orthogonal to the UCM space (non-motor equivalent, nME) reflect task-specific motion of the salient performance variable (Mattos et al. 2011, 2014).

A number of studies explored multi-muscle posture-stabilizing synergies (defined as neural mechanisms stabilizing salient performance variables, Latash 2008) within the framework of the UCM hypothesis (Krishnamoorthy et al. 2003b; Wang et al. 2006; Klous et al. 2010; Krishnan et al. 2010; Falaki et al. 2017; Piscitelli et al. 2017). Those studies addressed steady-state whole-body actions, such as voluntary sway, and preparation to an action or to a predictable perturbation (early postural adjustments and anticipatory postural adjustments). Analysis of synergies in those studies involved two steps. First, muscle groups with parallel scaling of activation levels were identified (muscle modes or M-modes, Krishnamoorthy et al. 2003a); note that many studies have addressed M-modes as “muscle synergies” (D’Avella et al. 2003; Ivanenko et al. 2004; Ting and Macpherson 2005; Tresch and Jarc 2009). We prefer the term “M-mode” to avoid confusion with action-stabilizing synergies defined within the UCM hypothesis. Second, indices of stability of the center of pressure (COP, the point of application of the resultant vertical force) coordinate were quantified using M-modes as elemental variables.

In the current study, we used unexpected perturbations of vertical posture in the anterior-posterior direction to explore links between synergy indices and postural stability. Note that applying an external perturbation is the most direct way to assess stability, which is defined as an ability of the system of interest to return to a state or trajectory following a perturbation. Based on the aforementioned studies, we expected indices of both structure of variance and motor equivalence to correlate with indices of stability of the COP coordinate in the anterior-posterior direction (Hypothesis 1). Within this hypothesis, we explored synergy indices within time intervals reflecting preparation to perturbation (initial steady state), time windows selected to reflect involuntary posture-stabilizing mechanisms such as reflex effects and pre-programmed reactions, and final steady state after the subjects were expected to stabilize posture. Note that analysis of motor equivalence in earlier studies of reaching documented synergic effects during early responses to unexpected perturbations (within 100 ms) that were discussed as reflections of involuntary mechanisms (Mattos et al.

2011, 2014). Based on those studies, we expected changes in the synergic structure to be significant within the first 100 ms following a perturbation (Hypothesis 2).

We also explored possible changes in indices of postural stability with direction of perturbation and predictability of the perturbation direction. Given the initial posture, we expected the perturbations in the forward and backward directions to differ in their posture destabilizing effects (Aruin and Latash 1995; Jones et al. 2008; Piscitelli et al 2017). Hence, we hypothesized that higher posture-stabilizing synergy indices would be seen during perturbations perceived by subjects as less challenging and associated within quicker recovery of the initial posture (Hypothesis 3).

Effects of perturbation predictability have been studied with respect to two characteristics, magnitude of the perturbation (Toussaint et al. 1998; Habib Perez et al. 2016; Forghani et al. 2017a,b) and its direction (Gilles et al. 1998; Piscitelli et al. 2017). No systematic effects of perturbation direction uncertainty on the latency and rate of increase of ground reaction forces were reported in a study with lateral body perturbations (Gilles et al. 2017). In contrast, predictability of the perturbation direction has been shown to affect posture-stabilizing synergies and patterns of anticipatory postural adjustments in conditions when the subject himself/herself triggered perturbations of known or unknown direction (Piscitelli et al. 2017). Based on the latter study, we expected higher stability indices in conditions when the subjects knew the perturbation direction in advance as compared to series of trials with random presentation of perturbations in the two directions (Hypothesis 4). We also expected predominance of co-activation patterns in the M-mode space in more challenging conditions (i.e., with unpredictable perturbation direction) compared to reciprocal patterns in the less challenging conditions (Hypothesis 5).

Methods

Participants

Nine healthy participants, five females and four males (age 29 ± 6 years old, body mass 70.2 ± 11.3 kg, height 1.69 ± 0.13 m; mean $\pm$ SD), without any neurological, muscular, and/or orthopedic conditions took part in this study. All participants were right-leg dominant based on their preferred leg for kicking a ball. All participants gave written informed consent prior to the study, which was approved by the Office for Research Protections of the Pennsylvania State University.

Apparatus

A force platform (AMTI, OR-6) was used to record three forces (F_X , F_Y , F_Z) and three moments (M_X , M_Y , M_Z). We used the force plate coordinate system which 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 (Figure 1). A 21" monitor was positioned at the eye level about 1 m away from the subject to provide real-time visual feedback on the AP and ML coordinates of the center of pressure (COP_{AP} and COP_{ML} , respectively). COP_{AP} displacement forward and

backward caused cursor motion up and down, respectively, while COP_{ML} motion caused the cursor to move left and right.

Surface muscle electrical activity (EMG) was recorded using a Trigno Wireless System (Delsys Inc., MA, USA). Active electrodes were fixed over the bellies of the following 13 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). EMG signals were pre-amplified and band-pass filtered (20–450 Hz) before being transmitted to a data collection desktop computer (Dell, Core™ i7, 2.93 GHz). A customized LabView program (National Instruments Corp., Austin, TX, USA) was used to collect EMG and force platform data with a sampling frequency of 1 kHz with 16-bit resolution (PCI-6225, National Instruments).

Procedure

Initially, subjects stood barefoot on the force platform with their feet in parallel at hip width. This foot position was marked on the platform to make this natural position consistent across all trials and conditions. Each experimental session consisted of four tasks: 1) quiet standing, 2) control trials, 3) voluntary body sway task, and 4) load-release task. During all tasks, subjects held their arms fully extended in front of them (shoulders flexed at 90° and elbows fully extended).

The quiet standing and control trials were performed to correct and normalize EMG signals (see the next section). A detailed description of the procedure is given in Danna-Dos-Santos et al. (2007). In the quiet standing task, subjects stood quietly on the force platform for 15 s. They were instructed to look at a fixed point on the wall in front of them. In control trials, subjects held a handle bar by grasping the two circular panels at each side of the bar with both hands, in the same position as described above for the quiet standing (Figure 1). The bar was connected via a pulley system to the 5-kg load to generate either a downward force (the load was suspended from the middle of the bar), or an upward force (the load was acting through the pulley system behind the subjects' body). The subjects were instructed to hold the load with fully extended arms and stand still for 10 s, without leaning forward or backward (controlled by the experimenter). A one-minute rest was provided between the two conditions.

In the voluntary body sway task, subjects swayed mainly about the ankle joints in the anterior–posterior direction (Danna-dos-Santos et al. 2007; Klous et al. 2010) while keeping their arms fully extended. The sway was paced by an auditory metronome at 0.5 Hz. Subjects performed continuous voluntary body sways between two horizontal lines (targets) on the monitor. The lines were set at ± 3 cm forward and backward, symmetrical with respect to the natural COP_{AP} coordinate. During this task, visual feedback was provided on the COP displacement as a 5-mm white circle on the monitor. The COP_{AP} and COP_{ML} were computed as (Winter et al. 1996):

$$COP_{AP} = - \frac{M_z + (F_y \cdot d_z)}{F_z} \quad (1)$$

$$COP_{ML} = \frac{M_x + (F_y \cdot d_z)}{F_z} \quad (2)$$

where d_z represents the distance from the surface to the platform origin (0.043 m). Following two to three practice trials, each subject performed three trials with 30-s rest periods between trials; the duration of each trial was 35 s. Subjects were asked to minimize movements in the ML direction and to keep full contact of both feet with the platform surface during the sway (watched by the experimenter). EMG and COP data from voluntary sway task were used to identify muscle groups with parallel changes in activation (M-modes) and to link changes in the magnitude of M-modes to COP displacements (Jacobian matrix, see later).

In the load-release tasks, subjects stood naturally as before and leaned forward such that their COP_{AP} matched a horizontal line 3 cm anterior from the initial COP_{AP} coordinate. Leaning forward was used to ensure non-zero background muscle activation, which was necessary to perform further analysis of multi-muscle synergies (as in earlier studies, Klous et al. 2010; Falaki et al. 2016). This initial posture was consistent across all trials.

Subjects held in extended arms a horizontal bar with two circular endplates. Two loads (2 kg each for men and 1.5 kg for women) were attached to the bar using electromagnetic locks. One load was attached directly to the bar while the other one was attached via the pulley system and was suspended behind the subjects' body (Figure 1). The experimenter used two switches to turn off one of the two electromagnets at an unpredictable time, which released one of the loads leading to a postural perturbation. After the perturbation, subjects were asked to return to the initial steady state posture as soon as possible and maintain the final posture for 10 s.

There were two perturbation directions: Backward (the load in front of the subject was released) and Forward (the load behind the subject was released). Within a block of trials, the subjects either knew which load would be released (predictable) or did not know (unpredictable). Hence, the experimental design included two main factors, direction of perturbation and predictability. We will refer to the conditions as BP (backward perturbation, predictable), FP (forward perturbation, predictable), UBP (unpredictable backward perturbation), and UFP (unpredictable forward perturbation). The order of the BP and FP series was randomized across subjects. Each block included 22 trials with 10-s rest intervals between trials and a 3-min break after each 11 trials. Within the unpredictable conditions, there were 22 backward and 22 forward perturbations presented in a balanced order. Subjects were explicitly asked not to try to guess which load would be released. To minimize fatigue, 5-min rest periods were provided between conditions. Prior to each of the

predictable conditions, subjects had five practice trials. The unpredictable conditions were always performed after finishing the predictable conditions to avoid biasing the subjects by the more challenging unpredictable conditions.

Data processing

All signals were processed offline using a customized MATLAB R2016a program (Mathworks Corp., Natick, MA, USA). The force plate signals were low-pass filtered at 10 Hz with 4-th order, zero-lag Butterworth filter. COP_{AP} and COP_{ML} were computed using standard procedures, Eqs. (1) and (2).

For the load-release task, trials when the body position was not maintained steady prior to the perturbation (load release) or EMG signals were corrupted (e.g., due to electrode-skin detachment) were removed from further analyses. The number of excluded trials per conditions was 4 ± 1 . The onset of load release (t_0) was identified as the point in time when the magnitude of the first time derivative of the vertical ground reaction force (dF_Z/dt) exceeded or dropped by 10% of its peak absolute magnitude in that particular trial. Visual inspection was used to confirm these values.

Raw EMG signals were band-pass filtered (20–360 Hz) with 2-nd order, zero-lag Butterworth filter and rectified. Later, a moving average 100-ms window was applied. EMG data were shifted 50 ms backward with respect to the force platform data for computations involving both EMG and COP data to account for the electro-mechanical delay (Corcos et al. 1992). Each EMG signal was corrected for background activity and normalized using the method described in previous studies (Krishnamoorthy et al. 2003a; Klous et al. 2010):

$$EMG_{norm} = \frac{EMG - EMG_{qs}}{EMG_{MAX}} \quad (3)$$

where EMG_{qs} is the average filtered EMG during the quiet standing trial computed within the time interval {6 s; 10 s} and EMG_{MAX} is the maximal EMG activity across control trials and voluntary sway tasks.

Analysis of $COP_{AP}(t)$

To quantify the subject's recovery after the perturbation, the COP_{AP} trajectory after the first peak, caused by the unloading, was fitted with an exponential curve over 6 s (Figure 2). This was done using averaged across trials COP_{AP} trajectory for each condition and subject separately. The time constant (τ) of the exponential curve and the overshoot of the second extremum of the COP_{AP} trajectory as compared to the fitted exponential curve (COP_2 , Figure 2) were computed for each subject and condition separately. In addition, we calculated the COP_{AP} root mean square error (RMS) across trials for each subject and condition. RMS was quantified over each 1-s time interval after the perturbation. For across-subject comparisons, these RMS values were normalized by the average value during the initial steady state, within the time interval $\{t_0-1000; t_0-500 \text{ ms}\}$. Note that, for this

analysis, individual trials were aligned by the COP_{AP} peak, not by the perturbation time (as in the following Figure 3).

Defining M-modes

We identified groups of muscles with parallel changes in their levels of activation, M-modes. For this purpose, EMG_{norm} signals from the three voluntary body sway trials were integrated over 50-ms time windows (EMG_{norm}). Principal component analysis (PCA) with factor extraction after Varimax rotation was applied to the IEMG_{norm} correlation matrix (Krishnamoorthy et al. 2003a, b) to transform the 13-dimensional muscle activation space into a three-dimensional factor (M-mode) space based on the Kaiser (1960) criterion and the requirement that each M-mode had to contain at least one muscle significantly loaded (with absolute magnitude of the loading value > 0.5; Hair et al. 1995).

We classified M-modes into “dorsal-M-modes” (with significantly loaded dorsal muscles), “ventral-M-modes” (with significantly loaded ventral muscles), and “mixed M-modes” (which commonly had RA significantly loaded), similarly to previous studies (Krishnamoorthy et al. 2003a, b; Danna-Dos-Santos et al. 2007; Krishnan et al. 2011).

Defining the Jacobian matrix

Linear relations between small changes in the magnitude of M-modes ($\mathbf{M}$) and the COP_{AP} displacement (ΔCOP_{AP}) were assumed (Krishnamoorthy et al. 2003b; Danna-dos-Santos et al. 2007). For each subject, multiple linear regression analysis without intercept was used to find the relation between $\mathbf{M}$ and COP_{AP} data from the body sway task, averaged over each 50-ms time window. For the linear regression analysis, $\mathbf{M}$ and COP_{AP} were filtered with a low-pass (2 Hz), 4-th order, zero-lag Butterworth filter:

$$\Delta \text{COP}_{AP} = k_1 \Delta M_1 + k_2 \Delta M_2 + k_3 \Delta M_3 \quad (4)$$

The coefficients of the multiple linear regression analysis defined the Jacobian matrix: $\mathbf{J} = [k_1 \ k_2 \ k_3]$.

Variance analysis

The framework of the UCM hypothesis (Scholz and Schöner 1999) was used to analyze synergies stabilizing COP_{AP} in the M-mode space. The UCM was estimated as the null-space of the $\mathbf{J}$ matrix. The inter-trial variance in the M-mode space was partitioned into two components, variance parallel to the UCM (V_{UCM} , with no effects on COP_{AP}) and variance orthogonal to the UCM (V_{ORT}). To quantify V_{UCM} and V_{ORT} , the residual mean-free vectors of M-modes ($\mathbf{M}_{demeaned}$) were calculated by subtracting the mean magnitude of the M-modes across trials ($\overline{\Delta \mathbf{M}}$) from the changes in the M-mode magnitudes ($\Delta \mathbf{M}$) for each subject and condition:

$$\Delta \mathbf{M}_{\text{demeaned}} = \Delta \mathbf{M} - \overline{\Delta \mathbf{M}} \quad (5)$$

For each time window, the vector $\mathbf{M}_{\text{demeaned}}$ was projected onto the UCM (f_{UCM}) and the orthogonal subspace (f_{ORT}):

$$\begin{aligned} f_{\text{UCM}} &= \sum_{i=1}^{n-d} \left(\epsilon_i^T \cdot \Delta \mathbf{M}_{\text{demeaned}} \right)^T \cdot \epsilon_i^T \\ f_{\text{ORT}} &= \Delta \mathbf{M}_{\text{demeaned}} - (f_{\text{UCM}})^T \end{aligned} \quad (6)$$

V_{UCM} and V_{ORT} , normalized per dimension of the respective spaces, were calculated as:

$$\begin{aligned} V_{\text{UCM}} &= \sigma_{\text{UCM}}^2 = \frac{1}{(n-d)N_{\text{trials}}} \sum_{i=1}^N f_{\text{UCM}}^2 \\ V_{\text{ORT}} &= \sigma_{\text{ORT}}^2 = \frac{1}{dN_{\text{trials}}} \sum_{i=1}^N f_{\text{ORT}}^2 \end{aligned} \quad (7)$$

where $n = 3$ is the dimensionality of the M-mode space, and $d = 1$ is the dimensionality of the performance variable (COP_{AP}). For further statistical comparisons, these indices were averaged within two intervals, $\{(t_0-1000) \text{ ms}; (t_0-500) \text{ ms}\}$ and $\{(t_0+5500) \text{ ms}; (t_0+6000) \text{ ms}\}$, reflecting steady states before and after the perturbation. Additionally, V_{UCM} and V_{ORT} were averaged within two intervals reflecting short-latency and middle-latency responses to the perturbation; $\{(t_0+25) \text{ ms}; (t_0+75) \text{ ms}\}$; and $\{(t_0+125) \text{ ms}; (t_0+175) \text{ ms}\}$. Data for one of the subjects were removed from statistical analysis because his V_{UCM} and V_{ORT} values were about an order of magnitude larger than in other subjects. An index of synergy (V) was calculated to quantify the relative amount of variance consistent with stabilizing COP_{AP} coordinates: $V = (V_{\text{UCM}} - V_{\text{ORT}})/V_{\text{TOT}}$, where V_{TOT} is total variance per dimension. For statistical analysis, V was transformed using Fisher's z-transformation, resulting in V_Z (Solnik et al. 2013).

Motor equivalence analysis

Analysis of motor equivalence (Mattos et al. 2011, 2014, 2015) quantifies the amount of deviations in the space of elemental variables (M-modes) in directions preserving (motor equivalent, ME) or changing (non-motor equivalent, nME) the performance variable, COP_{ap} . The M-mode vectors were averaged over 10-ms time window centered at 1000 ms prior to t_0 (steady state), 50 ms after t_0 , and 100 ms after t_0 . The small time windows (10 ms) were used because of quick EMG changes after the perturbation. Further, the deviations in the M-mode space were computed between the steady-state values and each of the values after t_0 ($\mathbf{M}_{50}$ and $\mathbf{M}_{100}$) to evaluate early responses to perturbation. These deviations were projected onto the null-space of $\mathbf{J}$ and its orthogonal complement for each subject and each condition. The length of these projections represented the ME (f_{ME} , within the UCM) and

nME (f_{nME} , orthogonal to the UCM) components, respectively. These values were further normalized by the square root of the corresponding dimensionality (cf. Mattos et al. 2011):

$$\begin{aligned} ME &= \frac{\|f_{ME}\|}{\sqrt{n-d}} \\ nME &= \frac{\|f_{nME}\|}{\sqrt{d}} \end{aligned} \quad (8)$$

In addition, ME and nME component magnitudes were computed between the initial steady state at 500 ms prior to t_0 and final steady state at 6000 ms after t_0 , averaged over 100-ms time windows. These values were computed for each subject and condition separately. Larger time windows were used in this analysis, 100 ms vs. 10 ms, because we did not expect quick changes in EMGs within the steady-state time intervals.

Indices of co-activation and reciprocal activation

Co-activation and reciprocal activation changes in the M-mode space were quantified as *C*-index and *R*-index, respectively (Slijper and Latash 2000, 2004). This computation was based on the fact (see Results) that, in all subjects, the first two M-modes represented a dorsal-M-mode and a ventral-M-mode. The magnitudes of the modes were computed by multiplying the corresponding eigenvector by the muscle activation vector for each time sample. Further, we integrated the magnitude of dorsal-M-mode and ventral-M-mode within the time interval that covered quick reactions to the perturbations: $\{t_0; t_0+400 \text{ ms}\}$. Since the baseline activity of the dorsal muscles was greater than that of the ventral ones, the *R*- and *C*-index were calculated as:

$$\begin{aligned} R - \text{index} &= \int (\text{dorsal} - M - \text{mode}) - \int (\text{ventral} - M - \text{mode}) \\ C - \text{index} &= 0, \text{ if } \int (\text{dorsal} - M - \text{mode}) \text{ and } \int (\text{ventral} - M - \text{mode}) \text{ have different sign;} \\ C - \text{index} &= \min \left[\left| \int (\text{dorsal} - M - \text{mode}) \right|, \left| \int (\text{ventral} - M - \text{mode}) \right| \right] \end{aligned} \quad (9)$$

For comparison across subjects, both *R*-index and *C*-index were normalized by their respective highest absolute magnitude across all trials performed by each subject.

Statistics

The data are presented in the text and figures as means $\pm$ standard errors (SE). All statistical tests were performed using SPSS (IBM Corp., Armonk, NY, USA). To test Hypotheses 1 and 3, two-way repeated-measures ANOVAs were performed to evaluate the effects of

Predictability (predictable and unpredictable), and *Direction* (backward and forward) on outcome indices of the COP_{AP} analysis (RMS, τ , and COP₂), synergy index (V_Z), and the index of motor equivalence (ME).

To test Hypothesis 2 and 4, three-way repeated-measures ANOVAs were performed to evaluate the effects of *Component* (ME and nME, or V_{UCM} and V_{ORT}), *Predictability*, and *Direction* on the indices of motor equivalence and structure of variance. Since *Predictability* had no main effects and there was no significant interaction in the indices of variance analysis, two-way repeated-measures ANOVA, *Component* $\times$ *Direction* was run on the averaged variances across the predictable and unpredictable conditions.

To test Hypothesis 5, two-way repeated-measures ANOVAs were performed to evaluate the effects of *Predictability*, and *Direction* on the *R*-index and *C*-index.

Prior to applying parametric statistics, the data were tested for statistical assumptions of normality and sphericity. In cases of violations of normality, log-transformation was used to satisfy the normality assumptions. In cases of violation of sphericity, degrees-of-freedom were corrected using Greenhouse-Geisser. For all statistical tests, the significance level was set at $p = 0.05$.

Results

Mechanical characteristics

Figure 3 shows the average time profiles of COP_{AP} and RMS across subjects during the unloading trials. Individual trials were aligned by the perturbation onset time (t_0). The absolute peak of COP_{AP} displacement immediately after perturbation was similar across conditions, on average 3.32 to 3.69 cm. However, all subjects reported that forward perturbations (FP and UFP) were more challenging than backward perturbations (BP and UBP). This was reflected in the COP_{AP} oscillations and RMS characteristics after the perturbation without obvious effects of predictability of perturbation direction.

Indeed, starting 3 s after the perturbation, RMS in the FP and UFP conditions were significantly greater than RMS in the BP and UBP conditions (effect of *Direction*, $F_{[1,8]} = 10.9$; $p < 0.01$ for both time intervals illustrated in Figure 4A), with no effect of *Predictability*. These effects persisted for the later time intervals; Figure 4 illustrates the data for the earliest (t_0+3) s and latest (t_0+5) s of these time intervals. Time constants (τ) of the exponential curves fitted to the COP_{AP} trajectory after the perturbation (see Methods) were not statistically different across conditions (0.33 ± 0.05 s). However, the difference between the second extremum of the COP_{AP} trajectory and its respective value on the fitted curve (COP_2) was significantly greater in the FP and UFP conditions as compared to the BP and UBP conditions (Figure 4B, $F_{[1,8]} = 10.0$; $p < 0.05$). There was no effect of *Predictability* and no interaction.

M-mode and Jacobian

PCA analysis of the EMG data during the sway task showed a consistent pattern of M-modes across subjects. The first three PCs explained, on average, $73.7 \pm 5.8\%$ of the total

variance in the original EMG_{norm} space. Table 1 represents the averaged muscle loadings for the three factors (M-modes). Significant loadings are shown in bold. In all subjects, the M1-mode consisted of significantly loaded dorsal muscles, while the M₂-mode included the ventral muscles and, sometimes, TFL. The third M-mode usually had only RA significantly loaded.

Linear regression analysis between the M-mode changes and resulting COP_{AP} deviations confirmed that each M-mode was a significant predictor of COP_{AP} shifts ($p < 0.01$). On average, the coefficient of determination of the regression $R^2 = 0.77 \pm 0.03$.

R-index and C-index

Figure 5 shows the typical EMG time profiles for selected agonist-antagonist pairs, averaged across trials following a perturbation in the FP and BP conditions (data for a representative subject are shown). The time profiles typically showed reciprocal changes within the agonist-antagonist pairs in BP, while the muscle pairs tended to show co-contraction patterns in FP. While Fig. 5 shows the EMG patterns for the predictable conditions only, similar features of the EMG patterns were seen in the matched unpredictable conditions. Overall, no significant main effects of *Predictability* were seen in analyses related to the main hypotheses of the study.

Our further analysis of muscle activation patterns was based on analysis of M₁- and M₂-modes rather than individual muscles. Figure 6 shows the M-mode time profiles in the BP, FP, UBP, and UFP conditions, averaged across subjects. Note the reciprocal M-mode patterns in the BP and UBP condition and co-contraction patterns in the FP and UFP conditions similar to those illustrated in Figure 5 for individual EMGs.

To quantify the reciprocal and co-activation M-mode patterns, we computed the *R*-index and *C*-index (see Methods). We found that the *R*-index was negative and the *C*-index was zero in BP and UBP, whereas both *R*-index and *C*-index were positive in FP and UFP (Table 2). In addition, the magnitude of the *R*-index was smaller in the FP and UFP conditions compared to the BP and UBP conditions. Statistical analysis revealed that the *R*-index and *C*-index magnitudes in BP and UBP were significantly smaller than those in FP and UFP (*R*-index: $F_{[1,8]} = 55.9$, $p < 0.001$; *C*-index: $F_{[1,8]} = 9.2$, $p < 0.05$). There were no effects of *Predictability* and no significant interaction.

Variance analysis

Figure 7 shows the time profiles of V_{UCM} and V_{ORT}, averaged across subjects for the BP and FP conditions; the variance patterns in the UBP and UFP conditions were similar to those illustrated in Figure 7. Note the increase in V_{ORT} right after the perturbation in the FP condition, whereas there was no comparable increase in the BP condition.

The magnitudes of V_{UCM} and V_{ORT} quantified in different time intervals are presented in Figure 8. During steady-state, 500 ms prior to the perturbation and at 50 ms after the perturbation, V_{ORT} was significantly greater than V_{UCM} (main effect of *Component*, $F_{[1,7]} = 8.7$; $p < 0.05$). This difference disappeared at 150 ms after the perturbation. At 150 ms after the perturbation, significant effects of *Direction* ($F_{[1,7]} = 26.3$; $p < 0.01$) and *Component* ×

Direction interaction ($F_{[1, 7]} = 7.0$; $p < 0.05$) were seen; the data for these earliest effects are illustrated in the left panel of Figure 8. V_{ORT} in the FP and UFP conditions was significantly greater as compared to the BP and UBP conditions; in addition, V_{ORT} was significantly greater than V_{UCM} in the FP and UFP conditions. At 6000 ms after the perturbation, significant effects of *Component* ($F_{[1, 7]} = 6.0$; $p < 0.05$), *Predictability* ($F_{[1, 7]} = 9.4$; $p < 0.05$), and *Direction* ($F_{[1, 7]} = 6.0$; $p < 0.05$) without interactions were found. The effects reflected $V_{ORT} > V_{UCM}$, and BP, FP > UBP, UFP (these effects are illustrated in the right panel of Figure 8). In addition, indices of variances in the FP and UFP conditions were significantly greater than those in the BP and UBP conditions.

The described features of V_{UCM} and V_{ORT} were also reflected in the z-transformed index of synergy, V_Z . In particular, V_Z in the BP and UBP conditions was significantly greater than in the FP and UFP conditions at 150 ms after the perturbation ($F_{[1, 7]} = 6.9$; $p < 0.05$), even though no significant effects were found in other phases (not illustrated).

Motor equivalence analysis

Analysis of motor equivalence revealed effects partly similar to those described in the analysis of the structure of inter-trial variance; this analysis, however, showed significant effects earlier than those described for the analysis of inter-trial variance (compare Figures 8 and 9). At the initial steady state, 500 ms prior to the perturbation, there were no significant effects of any of the factors. At 50 ms after the perturbation, significant effects of *Direction* ($F_{[1, 8]} = 6.7$; $p < 0.05$), *Predictability* ($F_{[1, 8]} = 10.1$; $p < 0.05$), and *Component* ($F_{[1, 8]} = 7.3$; $p < 0.05$) appeared without any interactions. These effects reflected $nME > ME$; both indices in predictable conditions were smaller than those in unpredictable conditions; and the indices in the FP and UFP conditions were greater than those in the BP and UBP conditions. At 100 ms after the perturbation, the effect of *Predictability* disappeared, but the effects of *Direction* ($F_{[1, 8]} = 36.2$; $p < 0.001$) and *Component* ($F_{[1, 8]} = 5.3$; $p < 0.05$) persisted. These effects are illustrated in the left panel of Figure 9; note that the time of these effects, $t_0 + 100$ ms, is earlier than the time of the earliest effects illustrated in Figure 8, $t_0 + 150$ ms. At 6000 ms after the perturbation, there was significant effect of *Component* ($F_{[1, 8]} = 10.3$; $p < 0.05$) reflecting $nME > ME$ and a significant *Component* $\times$ *Direction* interaction ($F_{[1, 8]} = 5.7$; $p < 0.05$). The interaction reflected higher ME for FP and UFP compared to BP and UBP ($p < 0.05$), while nME showed an opposite trend.

Discussion

Most of the main hypotheses formulated in the Introduction have been supported by the findings. In particular, perturbations in the forward direction (FP and UFP), compared to perturbations in the backward direction (BP and UBP), were characterized by smaller COP-stabilizing synergy indices (V_Z) and larger nME components. Similar effects were found in mechanical characteristics of the response to the perturbations, namely RMS and COP_2 had larger magnitudes for the perturbations in the forward direction. These observations support Hypothesis 1. Changes in the synergic structure were seen as early as 100-150 ms following the perturbation, while effects on the indices of motor equivalence were seen even earlier, about 50 ms after the perturbation, in support of Hypothesis 2.

Hypothesis 3 has also been supported: Higher posture-stabilizing synergy indices were seen for the perturbations in the backward direction, which was perceived as less challenging by subjects. Hypothesis 4, however, was not supported by the results as predictability of the perturbation direction had weak or no effects on the indices of stability. While forward perturbations were associated with co-activation patterns in both individual agonist-antagonist muscle pairs and in the M-mode space, backward perturbations resulted in reciprocal patterns as reflected in the *R*- and *C*-indices. So, that portion of Hypothesis 5 has been supported. However, we saw no effects of perturbation predictability on the *R*- and *C*-indices, against the prediction of Hypothesis 5. In summary, we observed very strong effect of perturbation direction on indices of activation patterns, M-mode synergies, and response mechanics, but limited or no effects of predictability of perturbation direction. Overall, these observations are in line with an earlier study, which reported no major effects of direction predictability in the analysis of the effects of lateral body perturbations (Gilles et al. 1998).

Further, we discuss the issue of postural stability within a hypothesis on hierarchical control of whole-body actions with spatial referent coordinates (RCs) for the involved effectors. We offer a novel interpretation on the role of co-activation patterns in postural control and discuss the contrasting effects of predictability on anticipatory and compensatory postural adjustments.

Postural stability: Synergic indices and mechanics

Vertical posture of the human body in the field of gravity is inherently unstable due to such factors as the relatively high center of mass, relatively small support area, multiple joints along the vertical body axis, and spontaneous changes in neuronal activity and muscle forces (reviewed in Winter et al. 1996; Mergner et al. 2003). These factors turn quiet standing into a complex neural control problem, which becomes even more complex in the presence of external perturbations. One of the approaches to the problem of postural stability has been developed within the framework of the UCM hypothesis (Scholz and Schöner 1999). According to this approach, the central nervous system arranges muscles into stable groups (M-modes, also addressed as “muscle synergies”, d’Avella et al. 2003; Ivanenko et al. 2004; Ting and Mcpherson 2004) and then stabilizes a subspace within the M-mode space that corresponds to a desired value of a salient performance variable, e.g., COP coordinate. This mode of control is expected to lead to a specific signature of inter-trial variance as well as to the phenomenon of motor equivalence (Scholz et al. 2007; Mattos et al. 2011). Both have been documented in recent studies of muscle activation patterns during whole-body tasks performed while standing (Danna-dos-Santos et al. 2007; Klous et al. 2011; Falaki et al. 2017).

Earlier studies documented multi-M-mode synergies stabilizing COP coordinate during steady-state tasks (Krishnamoorthy et al. 2003b; Klous et al. 2011). In our experiment, no such synergies were observed as reflected in greater components of the M-mode inter-trial variance affecting COP_{AP} (V_{ORT}) as compared to the variance that had no effect on COP_{AP} (V_{UCM}). This atypical signature could be due to the fact that the subjects expected a perturbation at an unpredictable time and were ready for a corrective action when it becomes necessary. These results may be seen as similar to observations of a long-lasting drop in the

synergy index in trials when a perturbation could be expected documented recently for multi-finger tasks (Ambike and Tillman 2017). Such feed-forward adjustments of posture-stabilizing synergies are similar to anticipatory synergy adjustments (ASAs, Olafsdottir et al. 2005; Klous et al. 2011; Krishnan et al. 2011) but differ from ASAs in their longer duration.

Earlier studies of multi-M-mode synergies stabilizing COP coordinate did not estimate postural stability using external perturbations and quantifying the mechanical response of the body (Krishnamoorthy et al. 2003b; Danna-dos-Santos et al. 2007; Klous et al. 2011). Indeed, the most direct method to test postural stability is to apply a perturbation and quantify the system's response. We used three characteristics of the mechanics of response to the standard perturbation, RMS, time constant of the exponent regression, and COP_2 . Two of these characteristics, RMS and COP_2 , showed larger magnitudes for perturbations in the forward direction (FP and UFP conditions) compared to perturbation in the backward direction (BP and UBP). Larger RMS reflects long-lasting, lingering effects of perturbation on the COP trajectory, while larger COP_2 may be seen as a sign of a more under-damped process during the forward perturbations compared to the backward ones. Note that these characteristics mirrored the subjects' reports that forward perturbations were perceived as more challenging.

Direction-specific differences were also observed in the two main characteristics of COP-stabilizing synergies. They were seen as soon as 100-150 ms after the perturbation and corresponded to relatively larger V_{ORT} components for the perturbation in the forward direction (FP and UFP) and, correspondingly, smaller synergy indices (V_Z) in those conditions compared to the conditions with perturbations in the backward direction (BP and UBP). Effects on the indices of motor equivalence (ME and nME) were seen even earlier, as early as 50 ms after the perturbation. Taken together, these results confirm a relation between the computed indices of synergic control and mechanical stability of posture following a perturbation.

Possible physiological mechanisms of posture-stabilizing synergies

A number of mechanisms contribute to stabilization of vertical posture in the presence of unexpected perturbations (reviewed in Maurer et al. 2006; Mergner 2007). These range from mechanical properties of muscles and other tissues providing immediate resistance to perturbations, to reflex and reflex-like muscle responses, and to voluntary postural corrections. Muscle mechanical properties can be tuned in anticipation of a perturbation (cf., “preflexes”, Loeb 1999), while other mentioned mechanisms – reactions to perturbations – contribute to feedback-based postural control. Our results suggest that even the earliest muscle responses to an unexpected perturbation could show signs of synergic organization reflected, in particular, in early changes in muscle activations (reflected in both ME and nME components) and in the structure of the inter-trial variance in the M-mode space (V_{UCM} , V_{ORT} , and V_Z). We believe that these are the first results showing that reflex and reflex-like muscle reactions to perturbations are organized with respect to stability of a particular mechanical variable, COP coordinate, relevant for the control of vertical posture.

A similar conclusion has been drawn in a study of multi-joint reaching perturbed by unexpected changes in the external resistance for one of the joints (Mattos et al. 2011, 2013).

Major ME deviations were observed in that study starting about 50 ms after the time when the perturbation produced measurable changes in movement kinematics. These results were confirmed by analysis in both joint configuration space and muscle activation space. Mattos and colleagues have concluded that the earliest ME kinematic responses were due to peripheral muscle properties tuned by the central nervous system to stabilize a salient performance variable, the endpoint trajectory,

Our results fit naturally a hypothesis on the control of movements with shifts of RCs, associated with subthreshold depolarization of neuronal pools (Feldman 2015), at different levels of the control hierarchy (Latash 2010). For the task of maintaining vertical posture, whole-body RC time profile is produced by scaling basic RC shifts (RC_{BASE}) uniting the main joints. A shift in a single RC_{BASE} leads to parallel scaling in activation levels of muscles crossing the involved joints; this is reflected in stable M-modes (or “muscle synergies”, reviewed in Tresch and Jarc 2009) observed in our study. Stability of such M-modes and their applicability to analysis of muscle activation patterns including several phases (such as the initial steady state, quick responses to the perturbation, and final steady state) has been discussed in earlier studies (Danna-dos-Santos et al. 2007, 2008; Torres-Oviedo and Ting 2010). An earlier study used sets of M-modes defined using various methods and obtained similar results (Klous et al. 2011). In our study, we defined M-modes using a standard task that required cyclical COP shifts. We also ran a pilot analysis of the data using two different sets of M-modes defined using the steady-state phase of the main task and the interval with fast EMG changes following the perturbation. The results were similar across those analyses (not presented in Results) suggesting that M-modes represented reflections of a relatively stable organization of control using RC_{BASE} .

Further, RC_{BASE} are translated into changes in RC for each joint (reflected in the r - and c -commands; Feldman 1980, 1986) and to RCs to individual muscles, which are equivalent to their thresholds of the stretch reflex (λ , as in the classical equilibrium-point hypothesis, Feldman 1966). This scheme involves a number of few-to-many transformations. According to the principle of abundance (Gelfand and Latash 1998; Latash 2012), these transformations are organized in a synergic way to stabilize salient performance variables. We do not know how these transformations are organized. Two philosophically different schemes have been suggested. Within the computational approach to motor control, synergic patterns have been discussed as consequences of optimal feedback control schemes (Todorov and Jordan 2002; Diedrichsen et al. 2010). Within the physical (physiological) approach (Latash 2016), such patterns have been modeled as consequences of back-coupling loops within the central nervous system or involving peripheral receptors (Latash et al. 2005; Martin et al. 2009).

The role of muscle co-activation in postural stability

Our experiments showed qualitatively different patterns of muscle activation in response to perturbations in different directions: While backward perturbation (BP and UBP) led to reciprocal patterns, forward perturbations (FP and UFP) resulted in co-activation patterns (see Fig. 5 and 6). These observations require analysis of the role of muscle co-activation.

If one considers a single joint, co-activating muscles leads to an increase in its apparent stiffness (e.g., Latash and Zatsiorsky 1993; Lee et al. 2006), which naturally is expected to

lead to stronger resistance to external forces. If one considers a multi-joint chain with an origin that is not fixed with respect to the environment, for example the human body standing in the field of gravity, effects of muscle co-activation on postural stability become complex and potentially detrimental. Here we define postural stability as an ability to stay within a vicinity of a desired body position, without falling or making a step, under brief external force perturbations and spontaneous changes in the intrinsic body states (for more detail see Latash and Zatsiorsky 2016). Consider the most direct effect of muscle co-activation, that is, an increase in the joint apparent stiffness. Co-activating muscles across all the major joints along the vertical body axis is expected to make the body more rigid. Is this good for postural stability? Consider two examples. First, a long log placed on one of its ends is very rigid and very unstable: It can be tipped over easily by a brief force applied to its upper end. Second, T'ai Chi experts commonly stand with their joints slightly flexed and muscles relaxed. They also show much better postural stability compared to the general populations (Gatts 2008). So, excessive muscle co-activation may not be such a good idea from the point of view of postural stability in the field of gravity.

Muscle co-activation looks unreasonable from many optimization approaches to motor control. Optimization approaches assume that problems of motor redundancy (Bernstein 1967) are solved by a computational process that selects a solution corresponding to a minimal value of a cost function. Numerous cost functions have been considered, and a number of those try to minimize costs related to muscle activations and/or forces (Uno et al. 1989; Crowninshield and Brand 1981; Alexander 2002; Prilutsky and Zatsiorsky 2002). In typical tasks, muscle co-activation has no effect on resultant mechanical variables, forces and moments of force, that lead to accelerations and changes in other kinematic variables. So, from the point of view of resultant mechanics, co-activation is wasteful, since the associated muscle activations consume energy, which is not contributing to the task.

However, humans do co-activate muscle excessively while standing in challenging conditions (Chen et al. 2015), which is reflected, in particular in the M-mode composition (Krishnamoorthy et al. 2004). Besides, populations with impaired motor abilities commonly show increased levels of muscle co-activation. This has been documented across various motor tasks for special populations ranging from persons with atypical development (Aruin and Almeida 1996), to healthy older adults (Lee et al. 2015), and to patients with a variety of neurological disorders (Arias et al. 2012; Mari et al. 2014). What could be the reason for this strategy given its lack of optimality and questionable contribution to postural stability?

We suggest that the main goal of co-activation of antagonist muscles is to keep the lowest level of control at a joint level and avoid shifting control to the level of single muscles (reviewed in Latash 2018). Consider, for simplicity, a single-degree-of-freedom joint crossed by only two muscles. The r - and c -commands are defined as the midpoint between the two λ values (r -command) and the range between the λ values (c -command, Figure 10A; Feldman 1980). If only one muscle crossing the joint is active (Figure 10B), i.e., in the absence of co-activation, the r - and c -commands become ill-defined (moreover, formally, the c -command becomes negative) because changes in the subthreshold λ of the opposing muscle (see the family of thin, dashed muscle torque-angle characteristics in Figure 10B) have no effect on the joint state. The joint state becomes sensitive to shifts in only one λ , and the controller

has to switch to a muscle-specific mode. This seems to be perfect time to present a quotation from Hughlings Jackson (1889): "... the central nervous system knows nothing about muscles, it knows only movements (p. 358)."

To avoid ambiguous situations, similar to those illustrated in Figure 10B, the controller has to ensure that both muscles are either within the activation zone (i.e., there is non-zero co-activation) or very close to the activation zone. Note that recent studies have documented bursts of muscle activation in response to small externally imposed motion of a joint that is naturally relaxed (e.g., Foisy and Feldman 2006; Raptis et al. 2010). In other words, λ s in relaxed muscles are naturally kept close to the activation threshold. In tasks that are perceived as challenging, the controller may prefer to facilitate visible co-activation to ensure that both muscles always remain within or close to their activation zones, even if the effector is moved by external forces.

This interpretation is corroborated by our current results showing that the subjects facilitated a co-activation response in conditions perceived by them as more challenging (FP and UFP) compared to the less challenging conditions (BP and UBP) characterized by a reciprocal pattern of activation. Along similar lines, an earlier study (Piscitelli et al. 2017) showed reciprocal patterns during anticipatory postural adjustments (APAs, Massion 1992) in conditions with predictable perturbation direction and co-activation patterns when perturbation direction was unpredictable and the task was more challenging. The aforementioned predominance of co-activation patterns in challenging conditions and in populations who may perceive typical tasks as challenging presents another illustration of the described strategy of ensuring that the c -command never drops far below zero.

Different effects of prior information on anticipatory and reactive control

Postural control involves both feed-forward and feedback mechanisms. The former include APAs, defined as changes in muscle activations and resultant forces seen about 100 ms prior to a perturbation triggered by the person's own action. The latter include both involuntary, reflex-like, responses (corrective postural adjustments, CPAs, Santos et al. 2010) and voluntary postural corrections. A number of recent studies have shown reciprocal links between APAs and CPAs: when APAs increase, CPAs tend to show a drop (Santos et al. 2010; Lee and Aruin 2014).

Our current results, together with an earlier study of self-triggered perturbations (Piscitelli et al. 2017), suggest very different effects of prior information on APAs and CPAs. Both studies used the same setup and the same unloading magnitudes. Both studies used predictable and unpredictable directions of perturbations. The only difference was in the way the timing of the perturbation was manipulated. In the earlier study, the subjects themselves triggered perturbations and, as a result, there was no ambiguity in the perturbation timing. In the current study, an experimenter triggered the perturbations, and the subject was unable to predict their timing. As a result, APAs were present in the earlier study and absent in the current one.

The study of Piscitelli and colleagues showed strong effects of predictability of perturbation direction on the patterns of muscle activation during APAs without effects on ASAs. In

particular, that study showed predominance of muscle co-activation patterns when the perturbation direction was unpredictable and predominance of reciprocal patterns for perturbations with predictable direction. These effects were similar across perturbations in the forward and backward directions. In contrast, the characteristics of ASAs were similar across perturbation directions and showed no effects of predictability of the perturbation direction.

In the current study, predictability of perturbation direction had virtually no significant main effects and interactions (cf. Gilles et al. 1998). This could be due to the very strong effects of perturbation direction that were seen in indices of co-activation and reciprocal activation in the space of M-modes, as well as in synergy indices. These effects could overpower possible effects of predictability.

Concluding comments

Overall, our study shows for the first time links between indices of postural stability quantified using mechanical responses to unexpected perturbations and indices of synergic control computed based on muscle activation signals: Both groups of indices showed similar effects of perturbation direction. In addition, the observation of qualitatively different patterns of muscle responses to perturbation in the two directions, forward and backward, suggest a different interpretation of the well-known phenomenon of muscle co-activation, in particular in whole-body postural tasks.

We have to admit a few limitations of our study. First, we explored perturbations in the anterior-posterior direction only. It is possible that better insights could be obtained in studies of postural stability in the medio-lateral direction, which is more challenging for tasks performed while standing (Dean et al. 2007). Our selection of the anterior-posterior direction was partly conditioned by the relatively few postural muscles with strong lateral action that can be recorded with surface electrodes. Our analysis was based on the notion of M-modes, which were defined based on a voluntary sway tasks (as in several earlier studies, Danna-dos-Santos et al. 2007; Klous et al. 2011). The extrapolation of the set of M-modes to the main task with load perturbations is not trivial. As mentioned earlier, we performed a pilot study with sets of M-modes defined in two different ways but found overall very similar results in all the main analyses. Nevertheless, we admit that the issue of M-mode generalization across tasks remains a weakness of the design.

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References

- Alexander MR. Energetics and optimization of human walking and running: the 2000 Raymond Pearl memorial lecture. *Amer J Hum Biol.* 2002; 14:641–648. [PubMed: 12203818]
- Ambike SS, Tillman M. Cue-induced changes in the stability of finger force-production tasks revealed by the uncontrolled-manifold analysis. *J Neurophysiol.* 2017; jn.00519.2017. doi: 10.1152/jn.00519.2017

- Arias P, Espinosa N, Robles-García V, Cao R, Cudeiro J. Antagonist muscle co-activation during straight walking and its relation to kinematics: insight from young, elderly and Parkinson's disease. *Brain Res.* 2012; 1455:124–131. [PubMed: 22502978]
- Aruin AS, Almeida GL. A coactivation strategy in anticipatory postural adjustments in persons with Down syndrome. *Motor Control.* 1996; 1:178–191.
- Aruin AS, Latash ML. Directional specificity of postural muscles in feed-forward postural reactions during fast voluntary arm movements. *Exp Brain Res.* 1995; 103:323–332. [PubMed: 7789439]
- Bernstein, NA. *The Co-ordination and Regulation of Movements.* Pergamon Press; Oxford: 1967.
- Chen B, Lee YJ, Aruin AS. Anticipatory and compensatory postural adjustments in conditions of body asymmetry induced by holding an object. *Exp Brain Res.* 2015; 233:3087–3096. [PubMed: 26195166]
- Corcos DM, Gottlieb GL, Latash ML, Almeida GL, Agarwal GC. Electromechanical delay: An experimental artifact. *J Electromyogr Kinesiol.* 1992; 2:59–68. [PubMed: 20719599]
- Crowninshield RD, Brand RA. A physiologically based criterion of muscle force prediction in locomotion. *J Biomech.* 1981; 14:793–801. [PubMed: 7334039]
- Danna-Dos-Santos A, Degani AM, Latash ML. Flexible muscle modes and synergies in challenging whole-body tasks. *Exp Brain Res.* 2008; 189:171–187. [PubMed: 18521583]
- Danna-Dos-Santos A, Slomka K, Zatsiorsky VM, Latash ML. Muscle modes and synergies during voluntary body sway. *Exp Brain Res.* 2007; 179:533–550. [PubMed: 17221222]
- d'Avella A, Saltiel P, Bizzi E. Combinations of muscle synergies in the construction of a natural motor behavior. *Nat Neurosci.* 2003; 6:300–308. [PubMed: 12563264]
- Dean JC, Alexander NB, Kuo AD. The effect of lateral stabilization on walking in young and old adults. *IEEE Trans Biomed Eng.* 2007; 54:1919–1926. [PubMed: 18018687]
- Diedrichsen J, Shadmehr R, Ivry RB. The coordination of movement: optimal feedback control and beyond. *Trends Cogn Sci.* 2010; 14:31–39. [PubMed: 20005767]
- Falaki A, Lewis MM, Huang X, Latash ML. Impaired synergic control of posture in Parkinson's patients without postural instability. *Gait Posture.* 2016; 44:209–215. [PubMed: 27004660]
- Falaki A, Huang X, Lewis MM, Latash ML. Motor equivalence and structure of variance: Multi-muscle postural synergies in Parkinson's disease. *Exp Brain Res.* 2017; 235:2243–2258. [PubMed: 28455740]
- Feldman AG. Functional tuning of the nervous system with control of movement or maintenance of a steady posture. II. Controllable parameters of the muscle. *Biophysics.* 1966; 11:565–578.
- Feldman AG. Once more on the equilibrium-point hypothesis (λ -model) for motor control. *J Mot Behav.* 1986; 18:17–54. [PubMed: 15136283]
- Feldman AG. Superposition of motor programs. I. Rhythmic forearm movements in man. *Neurosci.* 1980; 5:81–90.
- Feldman, AG. *Referent control of action and perception: Challenging conventional theories in behavioral science.* Springer; NY: 2015.
- Foisy M, Feldman AG. Threshold control of arm posture and movement adaptation to load. *Exp Brain Res.* 2006; 175:726–744. [PubMed: 16847611]
- Forghani A, Preuss R, Milner T. Postural response characterization of standing humans to multi-directional, predictable and unpredictable perturbations to the arm. *J Electromyogr Kinesiol.* 2017a; 32:83–92. [PubMed: 28061380]
- Forghani A, Preuss R, Milner TE. Effects of amplitude and predictability of perturbations to the arm on anticipatory and reactionary muscle responses to maintain balance. *J Electromyogr Kinesiol.* 2017b; 35:30–39. [PubMed: 28591642]
- Gatts S. Neural mechanisms underlying balance control in Tai Chi. *Med Sport Sci.* 2008; 52:87–103. [PubMed: 18487889]
- Gelfand IM, Latash ML. On the problem of adequate language in movement science. *Motor Control.* 1998; 2:306–313. [PubMed: 9758883]
- Gilles M, Wing AM, Kirker SG. Lateral balance organisation in human stance in response to a random or predictable perturbation. *Exp Brain Res.* 1999; 124:137–144. [PubMed: 9928835]

- Habib Perez O, Singer JC, Mochizuki G. The effects of predictability on inter-limb postural synchronization prior to bouts of postural instability. *Gait Posture*. 2016; 46:167–172. [PubMed: 27131196]
- Hair, JF., Anderson, RE., Tatham, RL., Black, WC. Factor analysis. In: Borkowski, D., editor. *Multivariate data analysis*. Prentice Hall; Englewood Cliffs: 1995. p. 364–404.
- Hughlings Jackson J. 1889, On the comparative study of disease of the nervous system. *Br Med J*. Aug 17.1889 :355–362.
- Ivanenko YP, Poppele RE, Lacquaniti F. Five basic muscle activation patterns account for muscle activity during human locomotion. *J Physiol*. 2004; 556:267–282. [PubMed: 14724214]
- Jones SL, Henry SM, Raasch CC, Hitt JR, Bunn JY. Responses to multi-directional surface translations involve redistribution of proximal versus distal strategies to maintain upright posture. *Exp Brain Res*. 2008; 187:407–417. [PubMed: 18299821]
- Kaiser HF. The application of electronic computers to factor analysis. *Educ Psychol Measure*. 1960; 20:141–151.
- Klous M, Mikulic P, Latash ML. Two aspects of feed-forward postural control: Anticipatory postural adjustments and anticipatory synergy adjustments. *J Neurophysiol*. 2011; 105:2275–2288. [PubMed: 21389305]
- Krishnamoorthy V, Goodman SR, Latash ML, Zatsiorsky VM. Muscle synergies during shifts of the center of pressure by standing persons: Identification of muscle modes. *Biol Cybern*. 2003a; 89:152–161. [PubMed: 12905043]
- Krishnamoorthy V, Latash ML, Scholz JP, Zatsiorsky VM. Muscle synergies during shifts of the center of pressure by standing persons. *Exp Brain Res*. 2003b; 152:281–292. [PubMed: 12904934]
- Krishnamoorthy V, Latash ML, Scholz JP, Zatsiorsky VM. Muscle modes during shifts of the center of pressure by standing persons: Effects of instability and additional support. *Exp Brain Res*. 2004; 157:18–31. [PubMed: 14985897]
- Krishnan V, Aruin AS, Latash ML. Two stages and three components of postural preparation to action. *Exp Brain Res*. 2011; 212:47–63. [PubMed: 21537967]
- Latash, ML. *Synergy*. Oxford Univ. Press; New York, NY: 2008.
- Latash ML. Motor synergies and the equilibrium-point hypothesis. *Motor Control*. 2010; 14:294–322. [PubMed: 20702893]
- Latash ML. The bliss (not the problem) of motor abundance (not redundancy). *Exp Brain Res*. 2012; 217:1–5. [PubMed: 22246105]
- Latash ML. Towards physics of neural processes and behavior. *Neurosci Biobehav Rev*. 2016; 69:136–146. [PubMed: 27497717]
- Latash ML. Muscle co-activation: Definitions, mechanisms, and functions. *J Neurophysiol*. 2018 in press.
- Latash ML, Scholz JP, Schöner G. Toward a new theory of motor synergies. *Motor Control*. 2007; 11:276–308. [PubMed: 17715460]
- Latash ML, Shim JK, Smilga AV, Zatsiorsky V. A central back-coupling hypothesis on the organization of motor synergies: a physical metaphor and a neural model. *Biol Cybern*. 2005; 92:186–191. [PubMed: 15739110]
- Latash ML, Zatsiorsky VM. Joint stiffness: Myth or reality? *Hum Move Sci*. 1993; 12:653–692.
- Latash, ML., Zatsiorsky, VM. *Biomechanics and Motor Control: Defining Central Concepts*. Academic Press; New York, NY: 2016.
- Lee PJ, Rogers EL, Granata KP. Active trunk stiffness increases with co-contraction. *J Electromyogr Kinesiol*. 2006; 216:51–57.
- Lee YJ, Aruin AS. Isolated and combined effects of asymmetric stance and pushing movement on the anticipatory and compensatory postural control. *Clin Neurophysiol*. 2014; 125:768–776. [PubMed: 24161607]
- Lee YJ, Chen B, Aruin AS. Older adults utilize less efficient postural control when performing pushing task. *J Electromyogr Kinesiol*. 2015; 25:966–972. [PubMed: 26403099]
- Loeb GE. What might the brain know about muscles, limbs and spinal circuits? *Prog Brain Res*. 1999; 123:405–409. [PubMed: 10635735]

- Mari S, Serrao M, Casali C, Conte C, Martino G, Ranavolo A, Coppola G, Draicchio F, Padua L, Sandrini G, Pierelli F. Lower limb antagonist muscle co-activation and its relationship with gait parameters in cerebellar ataxia. *Cerebellum*. 2014; 13:226–236. [PubMed: 24170572]
- Martin V, Scholz JP, Schöner G. Redundancy, self-motion, and motor control. *Neural Comput*. 2009; 21:1371–1414. [PubMed: 19718817]
- Massion J. Movement, posture and equilibrium – interaction and coordination. *Prog Neurobiol*. 1992; 38:35–56. [PubMed: 1736324]
- Mattos D, Latash ML, Park E, Kuhl J, Scholz JP. Unpredictable elbow joint perturbation during reaching results in multijoint motor equivalence. *J Neurophysiol*. 2011; 106:1424–1436. [PubMed: 21676927]
- Mattos D, Kuhl J, Scholz JP, Latash ML. Motor equivalence (ME) during reaching: Is ME observable at the muscle level? *Motor Control*. 2013; 17:145–175. [PubMed: 23370796]
- Mattos D, Schöner G, Zatsiorsky VM, Latash ML. Motor equivalence during accurate multi-finger force production. *Exp Brain Res*. 2015; 233:487–502. [PubMed: 25344311]
- Maurer C, Mergner T, Peterka RJ. Multisensory control of human upright stance. *Exp Brain Res*. 2006; 171:231–250. [PubMed: 16307252]
- Mergner T. Modeling sensorimotor control of human upright stance. *Prog Brain Res*. 2007; 165:283–297. [PubMed: 17925253]
- Mergner T, Maurer C, Peterka RJ. A multisensory posture control model of human upright stance. *Prog Brain Res*. 2003; 142:189–201. [PubMed: 12693262]
- Nashner LM. Organization and programming of motor activity during posture control. *Prog Brain Res*. 1979; 50:177–184. [PubMed: 551424]
- Nashner LM, Shupert CL, Horak FB, Black FO. Organization of posture controls: an analysis of sensory and mechanical constraints. *Prog Brain Res*. 1989; 80:411–418. [PubMed: 2699375]
- Olafsdottir H, Yoshida N, Zatsiorsky VM, Latash ML. Anticipatory covariation of finger forces during self-paced and reaction time force production. *Neurosci Lett*. 2005; 381:92–96. [PubMed: 15882796]
- Piscitelli D, Falaki A, Solnik S, Latash ML. Anticipatory postural adjustments and anticipatory synergy adjustments: Preparing to a postural perturbation with predictable and unpredictable direction. *Exp Brain Res*. 2017; 235:713–730. [PubMed: 27866261]
- Prilutsky BI, Zatsiorsky VM. Optimization-based models of muscle coordination. *Exer Sport Sci Rev*. 2002; 30:32–38.
- Raptis H, Burtet L, Forget R, Feldman AG. Control of wrist position and muscle relaxation by shifting spatial frames of reference for motoneuronal recruitment: possible involvement of corticospinal pathways. *J Physiol*. 2010; 588:1551–1570. [PubMed: 20231141]
- Santos MJ, Kanekar N, Aruin AS. The role of anticipatory postural adjustments in compensatory control of posture: 1. Electromyographic analysis. *J Electromyogr Kinesiol*. 2010; 20:388–397. [PubMed: 19660966]
- Scholz JP, Schöner G. The uncontrolled manifold concept: Identifying control variables for a functional task. *Exp Brain Res*. 1999; 126:289–306. [PubMed: 10382616]
- Scholz JP, Schöner G, Hsu WL, Jeka JJ, Horak F, Martin V. Motor equivalent control of the center of mass in response to support surface perturbations. *Exp Brain Res*. 2007; 180:163–179. [PubMed: 17256165]
- Slijper H, Latash ML. The effects of instability and additional hand support on anticipatory postural adjustments in leg, trunk, and arm muscles during standing. *Exp Brain Res*. 2000; 135:81–93. [PubMed: 11104130]
- Slijper HP, Latash ML. The effects of muscle vibration on anticipatory postural adjustments. *Brain Res*. 2004; 1015:57–72. [PubMed: 15223367]
- Solnik S, Pazin N, Coelho C, Rosenbaum DA, Scholz JP, Zatsiorsky VM, Latash ML. End-state comfort and joint configuration variance during reaching. *Exp Brain Res*. 2013; 225:431–442. [PubMed: 23288326]
- Ting LH, Macpherson JM. A limited set of muscle synergies for force control during a postural task. *J Neurophysiol*. 2005; 93:609–613. [PubMed: 15342720]

- Todorov E, Jordan MI. Optimal feedback control as a theory of motor coordination. *Nature Neurosci.* 2002; 5:1226–1235. [PubMed: 12404008]
- Torres-Oviedo G, Ting LH. Subject-specific muscle synergies in human balance control are consistent across different biomechanical contexts. *J Neurophysiol.* 2010; 103:3084–3098. [PubMed: 20393070]
- Toussaint HM, Michies YM, Faber MN, Commissaris DA, van Dieën JH. Scaling anticipatory postural adjustments dependent on confidence of load estimation in a bi-manual whole-body lifting task. *Exp Brain Res.* 1998; 120:85–94. [PubMed: 9628406]
- Tresch MC, Jarc A. The case for and against muscle synergies. *Curr Opin Neurobiol.* 2009; 19:601–607. [PubMed: 19828310]
- Uno Y, Kawato M, Suzuki R. Formation and control of optimal trajectory in human multijoint arm movement. *Biol Cybern.* 1989; 61:89–101. [PubMed: 2742921]
- Wang Y, Zatsiorsky VM, Latash ML. Muscle synergies in preparation to a step made under self-paced and reaction-time instructions. *Clin Neurophysiol.* 2006; 117:41–56. [PubMed: 16364687]
- Winter DA, Prince F, Frank JS, Powell C, Zabjek KF. Unified theory regarding A/P and M/L balance in quiet stance. *J Neurophysiol.* 1996; 75:2334–2343. [PubMed: 8793746]

Figure 1.

An illustration of the experimental setup. A: Control trials. EMG electrode placement is shown: 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). B: Load-release trials: two loads were attached to the bar using electromagnetic locks. Real-time visual feedback on the center of pressure (COP) coordinate was provided (panel C).

Figure 2.

Averaged across trials, time profiles of the center of pressure (COP) trajectory (solid black line, averages across trials) for a typical subject and the exponential regression curve (dashed red curve). Note that individual trials for this analysis were aligned by the COP_{ap} peak. Upper panel: FP (forward perturbation); Lower panel: BP (backward perturbation). COP_2 is defined as the distance between the second extremum of the COP trajectory and the exponential regression curve.

Figure 3.

Time profiles of the center of pressure (COP; A) and root mean square error (RMS; B). Averaged across subjects data are shown with standard error shades for the BP (backward perturbation; solid black lines), FP (forward perturbation, thin red lines), UBP (unpredictable backward perturbation, black dashed line), and UFP (unpredictable forward perturbation, thin dashed red line) conditions. Individual trials were aligned by the perturbation onset time (t_0 , shown by the vertical dashed lines). Note that the standard error shades are shown in one direction only for better visualization.

Figure 4.

A: Averaged across subjects RMS. White bars represent averaged RMS within $\{t_0 + 3 \text{ s}; t_0 + 4 \text{ s}\}$ interval, black bars represent averaged RMS within $\{t_0 + 5 \text{ s}; t_0 + 6 \text{ s}\}$ interval, and t_0 is the perturbation onset. B: Overshoot of the second extremum of the COP trajectory as compared to the fitted exponential curve (COP_2 , see Fig 2). Significant differences between the conditions with forward perturbations (FP and UFP) and conditions with backward perturbations (BP and UBP) are shown with one star ($p < 0.05$) and two stars ($p < 0.01$). For abbreviation, see the caption for Fig. 3.

Figure 5.

EMG time profiles averaged across trials for a typical subject in two predictable conditions: BP (left panels) and FP (right panels). Similar features of the EMG patterns were seen in the matched unpredictable conditions, UBP and UFP. The vertical dashed lines show the perturbation onset (t_0). The standard error shades are shown in one direction only for better visualization. TA – tibialis anterior; SOL – soleus; BF – biceps femoris; and RF – rectus femoris.

Figure 6.

The time profiles of M₁-mode (solid black lines) and M₂-mode (dashed red lines), averaged across subjects within each of the four conditions: BP, FP, UBP, and UFP. The shade represents the standard error. The vertical dashed lines show the perturbation onset (t₀). For abbreviation, see the caption for Fig. 3.

Figure 7.

The time profiles of the two indices of inter-trial variance analysis, V_{UCM} (top) and V_{ORT} (bottom), averaged across subjects with standard error shades. Solid black line – BP, dashed red lines – FP. The vertical dashed lines show the perturbation onset (t_0). The standard error shades are shown in one direction only for better visualization. For abbreviation, see the caption for Fig. 3.

Figure 8.

Averaged indices of inter-trial variance across subjects with standard error bars: V_{UCM} (white bars) and V_{ORT} (black bars) are shown for four phases, (t₀ - 500) ms, (t₀ + 50) ms, (t₀ + 150) ms, and (t₀ + 6000) ms. Statistically significant difference are shown with one star (p < 0.05) and two stars (p < 0.01). The vertical dashed lines show the perturbation onset (t₀). For abbreviation, see the caption for Fig. 3.

Figure 9.

Averaged indices of motor equivalence analysis across subjects with standard error bars: ME (white bars) and nME (black bars) are shown for four phases, ($t_0 - 500$) ms, ($t_0 + 50$) ms, ($t_0 + 100$) ms, and ($t_0 + 6000$) ms. Statistically significant difference are shown with one star ($p < 0.05$) and two stars ($p < 0.01$). For abbreviation, see the caption for Fig. 4.

Figure 10.

An illustration of the torque-angle characteristics of two muscles, agonist (positive torque values) and antagonist (negative torque values). A: The definition of the r - and c -commands when there is non-zero muscle co-activation. B: When there is no overlap of the muscle activation zones, changing threshold of the stretch reflex for the antagonist (λ_{ANT}) leads to changes in both r - and c -commands without a change in the joint state (see the family of dashed antagonist characteristics). The only way to control the joint effectively is to shift the control variable for the agonist muscle (λ_{AG}).

Table 1
Results of M-mode identification

	M1-mode	M2-mode	M3-mode
TA	-0.390 (0.069)	0.675 (0.038)	-0.002 (0.026)
SOL	0.869 (0.012)	-0.212 (0.056)	-0.031 (0.020)
GL	0.883 (0.008)	-0.174 (0.035)	-0.012 (0.013)
GM	0.873 (0.021)	-0.245 (0.041)	0.004 (0.029)
BF	0.831 (0.026)	-0.109 (0.073)	-0.074 (0.029)
ST	0.857 (0.015)	-0.213 (0.034)	-0.023 (0.010)
RF	-0.413 (0.044)	0.626 (0.079)	0.105 (0.086)
VL	-0.382 (0.053)	0.759 (0.034)	0.024 (0.025)
VM	-0.223 (0.055)	0.705 (0.048)	0.161 (0.085)
TFL	0.086 (0.053)	0.622 (0.036)	-0.101 (0.073)
ESL	0.752 (0.029)	-0.296 (0.045)	0.018 (0.022)
EST	0.744 (0.029)	-0.290 (0.035)	0.024 (0.026)
RA	-0.009 (0.029)	0.012 (0.050)	0.941 (0.025)

Loading factors (averages across subjects with standard errors in parentheses) are shown for the individual muscles. Significant loadings (>0.5) are shown in bold. Note the consistent patterns with dorsal muscles significantly loaded in the M1-mode and ventral muscles significantly loaded in the M2-mode. TA – tiobialis anterior; SOL – soleus; GL and GM – lateral and medial heads of gastrocnemius; BF – biceps femoris; SM – semitendinosus; RF – rectus femoris; VL and VM – lateral and medial vastii; TFL – tensor facsia latae; ESL and EST – lumbar and thoracic portions of erector spinae; and RA – rectus abdominis.

Table 2
Results of analysis of the reciprocal and co-activation indices

	BP	FP	UBP	UFP
<i>R</i> -index	-0.115 (0.008)	0.007 (0.019)	-0.110 (0.0007)	0.073 (0.020)
<i>C</i> -index	0 (0)	0.037 (0.013)	0 (0)	0.042 (0.014)

The averaged across subjects magnitude of the reciprocal (*R*-index) and co-activation (*C*-index) are presented with standard errors in parentheses for each of the four conditions: BP – backward perturbation; FP – forward perturbation, UBP – unexpected backward perturbation; and UFP – unexpected forward perturbation.