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RESEARCH ARTICLE

Anticipatory postural adjustments and anticipatory synergy adjustments: preparing to a postural perturbation with predictable and unpredictable direction

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Abstract We explored two aspects of feed-forward postural control, anticipatory postural adjustments (APAs) and anticipatory synergy adjustments (ASAs) seen prior to self-triggered unloading with known and unknown direction of the perturbation. In particular, we tested two main hypotheses predicting contrasting changes in APAs and ASAs. The first hypothesis predicted no major changes in ASAs. The second hypothesis predicted delayed APAs with predominance of co-contraction patterns when perturbation direction was unknown. Healthy subjects stood on the force plate and held a bar with two loads acting in the forward and backward directions. They pressed a trigger that released one of the loads causing a postural perturbation. In different series, the direction of the perturbation was either known (the same load released in all trials) or unknown (the subjects did not know which of the two loads would be released). Surface electromyograms were recorded and used to quantify APAs, synergies stabilizing center of pressure coordinate (within the uncontrolled manifold hypothesis), and ASA. APAs and ASAs were seen in all conditions. APAs were delayed, and predominance of co-contraction patterns was seen under the conditions with unpredictable direction of perturbation. In contrast, no significant changes in synergies and ASAs were seen. Overall, these results show that feed-forward control of vertical posture has two distinct components, reflected in APAs and ASAs, which show qualitatively different adjustments with changes in predictability of the direction of perturbation. These results are interpreted within the recently proposed hierarchical scheme of the synergic control of motor tasks. The observations underscore the complexity of the feed-forward postural control, which involves separate changes in salient performance variables (such as coordinate of the center of pressure) and in their stability properties.

Keywords Posture · Feed-forward control · Synergy · Anticipatory postural adjustment · Anticipatory synergy adjustment

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Introduction

Maintaining vertical posture by humans is a challenging mechanical task given the relatively high location of the center of mass and relatively small support area. In this study, we focus on feed-forward mechanisms of postural control acting when a standing person is subjected to a predictable, frequently self-initiated, perturbation (e.g., making a fast arm movement or releasing a load). One of these mechanisms, anticipatory postural adjustments (APAs), has been known for about half a century. Since the original study by Belenkiy et al. (1967), many researchers explored APAs using different methods to identify and quantify them (reviewed in Massion 1992, 1998; Latash and Hadders-Algra 2008). APAs represent changes in the activation levels of postural muscles in preparation to a self-initiated action associated with perturbation of the vertical posture. Such changes are typically seen starting about 100 ms prior

to the action initiation. Their function has been assumed to generate net forces and moments counteracting those expected from the perturbation (Cordo and Nashner 1982; Bouisset and Zattara 1987; Ramos and Stark 1990). Consistent with this hypothesis, APAs change their patterns when the direction of perturbation changes (Aruin and Latash 1995).

The second feed-forward mechanism, anticipatory synergy adjustments (ASA), has been described relatively recently (Olafsdottir et al. 2005; Shim et al. 2005). During whole-body tasks performed by standing persons, ASAs represent changes in an index of a multi-muscle synergy stabilizing the coordinate of the center of pressure (COP). Such changes may be seen in young, healthy persons about 200–300 ms prior to the action initiation (Klous et al. 2011; Krishnan et al. 2011, 2012), significantly earlier than APAs. The purpose of ASAs has been assumed to be twofold. First, ASAs facilitate a change in a salient performance variable, such as COP coordinate. Second, ASAs allow the actor to avoid fighting one's own synergies stabilizing that variable. Note that similar ASAs are expected independently of the direction of a perturbation, e.g., forward or backwards, since a quick reactive COP shift in the anterior–posterior direction is needed to stabilize posture across conditions.

The two mechanisms, APAs and ASAs, may be expected to show different degrees of specificity with changes in the direction of a self-triggered perturbation. To explore this prediction, we compared APAs and ASAs in standing subjects who performed similar actions that could lead to postural perturbations in two opposite directions. In some series, the subjects knew the direction of the perturbation in advance, while in other series, this direction varied randomly across trials. Our Hypothesis 1 was that ASAs would not show changes in their characteristics across series with known and unknown directions of perturbation (based on a study of multi-finger synergies, Zhou et al. 2013).

In contrast, our second hypothesis was that APAs would be sensitive to information on direction of perturbation. For trials with perturbations with randomly changing direction, we expected two changes in APAs as compared to conditions with known perturbation direction. First, APAs could be delayed, and even disappear (Hypothesis 2A) since a strong APA in a "wrong direction" could contribute to postural destabilization. Second, APAs could change their patterns. While young, healthy persons typically show reciprocal patterns of activation in agonist–antagonist postural muscle pairs during APAs (Bouisset and Zattara 1987; Aruin and Latash 1995), persons with impaired postural control tend to show parallel changes in activation of agonist–antagonist muscles (co-contraction patterns; Woollacott et al. 1988; Schmitz et al. 2002; Chen et al. 2015). Co-contracting agonist–antagonist muscles produces little net force/moment, but increases the apparent stiffness of the joint (Latash and Zatsiorsky 1993), which reduces kinematic consequences of any force perturbation. So, we also expected a change from a typical reciprocal APA pattern in conditions with known direction of perturbation to a co-contraction pattern in conditions when the direction of perturbation was unpredictable (Hypothesis 2B).

To test these hypotheses, we quantified APAs and ASAs in subjects performing a load-release task, which is typically associated with pronounced APAs (cf. Aruin and Latash 1995). ASAs were analyzed using the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999; reviewed in Latash et al. 2007; Latash 2008). This method quantifies inter-trial variance within a set of elemental variables (M-modes, muscle groups with parallel changes in activation levels, Krishnamoorthy et al. 2003a) in directions that lead to no changes in a salient performance variable (UCM for that variable) and in directions orthogonal to the UCM (ORT) leading to changes in the salient variable. Further, an index of synergy is computed reflecting the difference between the variance components, $\Delta V = (V_{UCM} - V_{ORT})/V_{TOT}$ normalized by total variance (V_{TOT}). Multi-M-mode synergies were quantified for COP coordinate in the anterior–posterior direction (COP_{AP}) as the salient performance variable.

Methods

Subjects

Eleven healthy subjects (six males and five females, age 28.5 ± 4.7 years, mass 67.95 ± 11.66 kg, and height 1.67 ± 0.10 m; mean ± SD) without any known musculoskeletal or neurological impairments took part in the experiment. All participants were right-handed based on their own disclosure about preferential hand use during daily activities such as writing and eating. All subjects gave their informed consent according to the procedures approved by the Office for the Research Protections of the Pennsylvania State University.

Apparatus

A force platform (AMTI, OR-6) was used to record the vertical, anterior–posterior, and medio-lateral components of the ground reaction force (F_Z, F_X, and F_Y, respectively) as well as the moments of force around the frontal and sagittal axes (M_Y and M_X, respectively). Surface muscle activation (EMG) signals were recorded using a 16-channel Trigno Wireless System (Delsys Inc., MA, USA). Active electrodes with built-in amplifiers (rectangular shape, 37 mm × 26 mm × 15 mm) were attached with adhesive

tape to the skin over the bellies of the following 13 muscles on the right side of the body: tibialis anterior (TA), soleus (SOL), gastrocnemius lateralis (GL), gastrocnemius medialis (GM), biceps femoris (BF), semitendinosus (ST), rectus femoris (RF), vastus lateralis (VL), vastus medialis (VM), tensor fasciae latae (TFL), lumbar erector spinae (ESL), thoracic erector spinae (EST), and rectus abdominis (RA). The electrode placement was confirmed by asking the subjects to perform a set of isomeric contractions and related free movements while observing the resulting EMG patterns (Kendall et al. 2005). EMG signals were pre-amplified and band-pass filtered (20–450 Hz) before being transmitted to the base station connected to the data collection computer (Dell, Core i7 2.93Ghz). A customized LabVIEW-based software (LabVIEW 2013—National Instruments, Austin, TX, USA) was used to acquire and record EMG and force platform signals sampled at 1 kHz with 16-bit resolution data acquisition board (PCI- 6225, 250 kS/s, 80 Analog Inputs Multifunction DAQ, National Instruments).

Procedures

In the initial position, subjects were standing barefoot on the force platform with their feet in parallel at hip width (the insides of the feet 15 cm apart). This foot position was marked on the top of the platform to make this initial position consistent across all trials and conditions. A 21-inch monitor positioned 1.5 m in front of the participants at the eye level was used for visual feedback. Each experimental session consisted of four tasks: (1) quiet standing, (2) control trials, (3) voluntary body sway task, and (4) load-release task.

The quiet standing and control trials were performed to normalize EMG signals (see the next section). A detailed description of the procedure is given in Danna-Dos-Santos et al. (2007). Briefly, in the quiet standing task, subjects were instructed to stand quietly on the force platform with arms by sides and to look at a fixed point on the wall in front of the subject, while trying to prevent any body movements for 30 s. In the control trials, subjects were asked to hold a handle bar by grasping the two circular panels at each side of the bar with both hands with the shoulders flexed at 90° and elbows fully extended (Fig. 1a). The bar was connected to a pulley system that allowed using the 5-kg load to generate either a downward force (the load was suspended from the middle of the bar; control trial #1) or an upward force (the load was acting through the pulley system behind the subject's body; control trial #2). This posture was held for at least 10 s with a one-minute rest period between the two conditions. During both control trials, the subjects were asked to stand still, without forward or backward movement (controlled by the experimenter).

In the voluntary body sway task, subjects were instructed to occupy an initial position with the arms crossed over the chest and fingertips placed on the shoulders and to perform continuous voluntary full-body sways about the ankle joints in the anterior–posterior (AP) direction (Danna-dos-Santos et al. 2007; Klous et al. 2011). The frequency of the sway was set at 0.5 Hz, paced by an auditory metronome. A continuous visual feedback was provided on the subjects' center of pressure (COP) displacement, in the anterior–posterior (COP_{AP}), and in the medial–lateral direction (COP_{ML}). These were computed online using the following equations (Winter et al. 1996):

$$\mathrm{COP_{AP}} = -\frac{M_y + (F_x \cdot d_z)}{F_z} \tag{1}$$

$$\mathrm{COP_{ML}} = \frac{M_x + \left(F_y \cdot d_z\right)}{F_z} \tag{2}$$

In these equations, d_z represents the distance from the surface to the platform origin (0.043 m). The amplitude of COP_{AP} shift displayed on the monitor was set at ±3 cm forward and backward, symmetrical with respect to the initial COP_{AP} coordinate. The target amplitude was presented on the screen as a pair of target lines while the instantaneous COP coordinate was shown as a 5-mm white circle. A period of practice was given to each subject prior to data acquisition. Only predictable conditions were used during this familiarization period. The task was performed twice; the duration of each trial was 30 s with a 30-s rest period between trials. Subjects were asked to do their best to minimize COP deviations in the medio-lateral direction and to keep full contact of both heels and toes with the platform surface during the sway (observed by the experimenter).

In the load-release tasks, subjects occupied the initial body position while holding the handle bar, in the same position as described above for the control trials. Then, they were requested to lean forward, such that their COP_{AP} matched a target line 3 cm from the initial COP_{AP} coordinate. They kept this position steadily for about 2–3 s. Leaning forward was used to ensure a nonzero level of background muscle activation, which was necessary to perform further analysis of multi-muscle synergies (as in earlier studies, Klous et al. 2011; Falaki et al. 2016). While leaning may lead to changes in APAs, these changes are relatively modest (Aruin et al. 1998; Aruin 2003). The initial posture was consistent across conditions with predictable and unpredictable directions of unloading (see later).

Two loads of 2 kg each were attached to the pulley system in such a way that one load was in front of the subject and the other load was behind the subject's body (Fig. 1b); as a result, there was no net vertical force acting on the handle. Each load was attached with a cylindrical

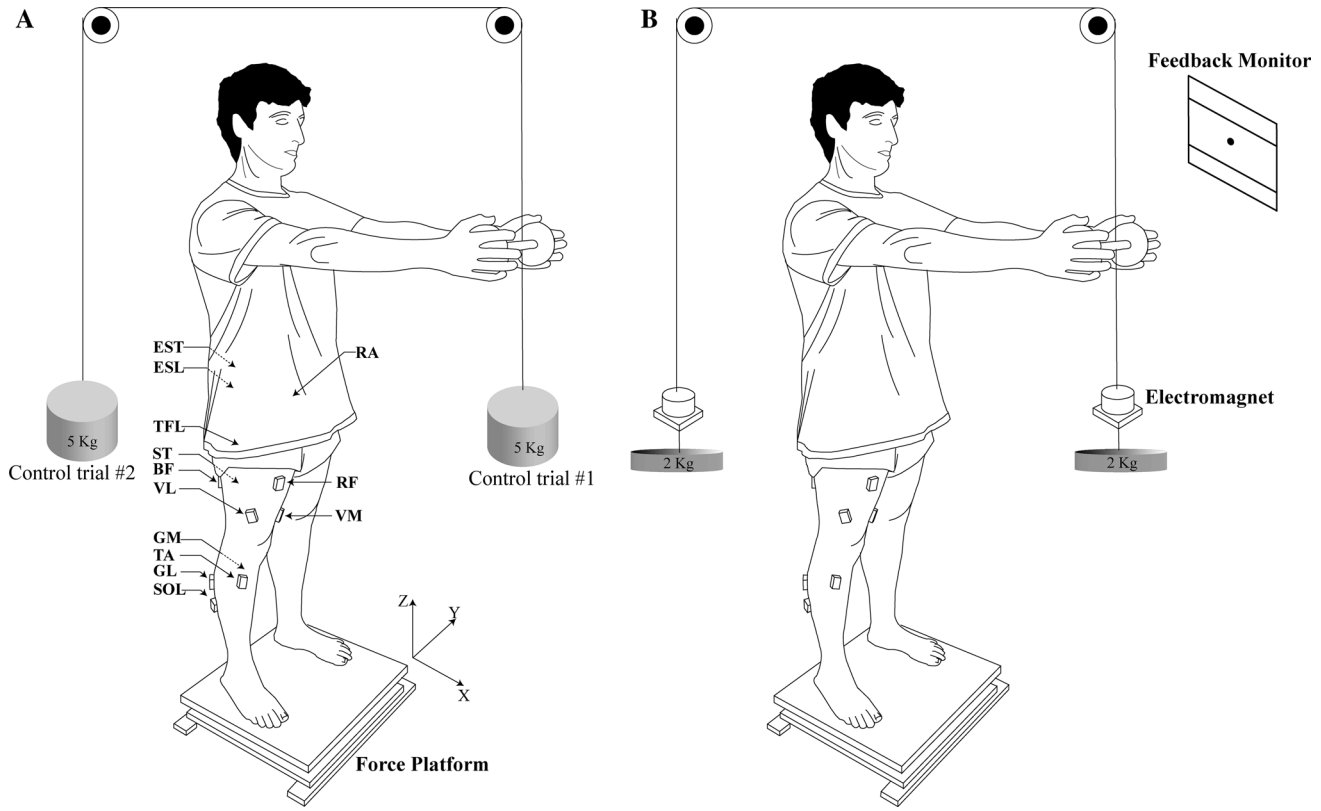


Fig. 1 **a** Schematic illustration of the control trials. In the control trial #1, a load (5 kg) was suspended from the middle of the bar in front of the subject. In the control trial #2, the load was connected through the pulley system behind the subject's body. **b** Schematic representation of the load-release trials. Subjects triggered perturbation by releasing a load (2 kg) attached to the electromagnets through the pulley system. Location of the EMG electrodes is shown (*TA* tibialis anterior, *SOL* soleus, *GM* gastrocnemius medialis, *GL* gastrocnemius lateralis, *BF* biceps femoris, *ST* semitendinosus, *RF* rectus femoris, *VL* vastus lateralis, *VM* vastus medialis, *TFL* tensor fasciae latae, *RA* rectus abdominis, *EST* thoracic erector spinae, *ESL* lumbar erector spinae)

electromagnet. On the right side of the handle bar, there was a switch that could turn off one of the two electromagnets releasing the corresponding load and leading to a postural perturbation. After reaching the initial steady state, subjects were asked to push the trigger with the right thumb to initiate the load release; this was done in a self-paced manner at any time within a 10-s time window.

The experimenter controlled which of the two electromagnets would be turned off by the switch. Two perturbation directions were studied: backward (the released load was in front of the subject) and forward (the released load was behind the body of the subject), under two different conditions where the perturbation direction was either known (Kn) or unknown (Un) to the subject in advance. We will refer to the conditions as BKn (backward perturbation, known direction), FKn (forward perturbation, known direction), BUn (backward perturbation, unknown direction), and FUn (forward perturbation, unknown direction). There were 24 trials within each experimental series. The direction of perturbation was kept the same and known to the subject in advance within the series BKn and FKn. The order of these two series was randomized across subjects. Two more series included perturbations with directions presented in an unpredictable, balanced order. Over these two series, 24 trials were under the BUn condition and 24 trials—under the FUn condition. In these series, the experimenter asked the subjects not to guess/predict the direction of the load release. In summary, participants always knew in advance the exact timing of the "perturbation" as it was self-triggered, while the direction could be either predictable or unpredictable. The intervals between the 15-s trials were 8–10 s (2–3 trials per minute) with 3-min rest period between conditions; the unpredictable conditions were always presented after the predictable conditions to avoid possible effects of performing the relatively unusual unpredictable conditions on the more familiar predictable conditions.

Prior to data collection, a period of familiarization with the load-release task, with 12 trials for each of the perturbation directions, was given to each subject. Additional rest periods were provided if requested, and none of the subjects reported fatigue. The whole experimental session lasted for about 90 min.

Data processing

The data were processed and analyzed off-line using a customized MATLAB 2015b (Mathworks, Natick, MA, USA) software package. Signals from the force platform were filtered with the 5-Hz low-pass, second-order, zero-lag Butterworth filter before calculating the COP coordinates using Eqs. (1) and (2).

For each 30-s trial of the body sway task, the data in the interval {3; 28 s} were accepted to avoid edge effects. A cycle was defined as the time between two successive anterior-most COP_{AP} coordinates. On average, each subject performed 12 full cycles within this period.

The onset of the load-release task (t_0) was calculated by a computer algorithm as the point in time when the magnitude of the first time derivative of F_Z exceeded 5% of its peak absolute magnitude in that particular trial. These values were confirmed by visual inspection.

For the load-release task, trials with the following errors were excluded from further analysis: Body position was not kept steady prior to t_0 (i.e., COP_{AP} trajectory exceeded ±2 standard deviations within the time interval {t_0-300 ms; t_0} from the average value of that particular series) and trials with corrupted EMG signals (likely due to electrode–skin detachment). We emphasized reproducible performance within the 300-ms interval prior to t_0 because this interval included both APAs and ASAs and was crucial for our analysis. The number of rejected trials per series was 5 ± 1.

Raw EMG signals were full-wave rectified and low-pass filtered by means of a moving average 100-ms window. To account for the electromechanical delay (Corcos et al. 1992), EMG data were shifted 50 ms backward with respect to the force platform data for computations involving both EMG and mechanical signals. In order to compare EMG data across subjects, the processed signals were corrected for background activity and normalized using the method described in previous studies (Krishnamoorthy et al. 2003a; Klous et al. 2010):

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

EMG_{qs} is the average filtered EMG during the quiet stance trial computed within the time interval {13 s; 17 s} and EMG_{ref} is the average filtered EMG in the middle of control trials. For dorsal muscles (SOL, GL, GM, BF, ST, ESL, and EST), EMG_{ref} was calculated from the control trial#1 in which the load was held in front of the subject and for the ventral muscles (TA, VM, VL, RF, RA, and TFL) when the load was acting behind the subject (control trial#2).

Defining muscle modes

The objective of this phase was to identify groups of muscles (muscle modes or M-modes, eigenvectors in the muscle activation space) that showed parallel scaling of changes in their levels of activation. Such muscle groups play the role of elemental variables for the analysis of synergies (see later and Krishnamoorthy et al. 2003a, b). This step reduced the 13-dimensional muscle activation space into a four-dimensional M-modes space. For this purpose, EMG_{norm} signals from the two voluntary body sway tasks were integrated over 50-ms time windows ($IEMG_{norm}$). For each subject, the $IEMG_{norm}$ data from the two trials were concatenated to create a matrix with 13 columns representing 13 muscles and the number of rows corresponding to the number of samples across the sway cycles analyzed. Principal component analysis with varimax rotation, and factor extraction was applied to the correlation matrix of $IEMG_{norm}$ data (Krishnamoorthy et al. 2003a, b; Danna-dos-Santos et al. 2007). For each subject, the first four principal components (PCs) were selected based on the following criteria: the Kaiser criterion and an inflection point in the scree plot after the fourth eigenvalue confirmed by visual inspection, and each PC had to contain at least one muscle with a significantly high loading (with the absolute magnitude over 0.5; Hair et al. 1995).

This procedure produced an orthogonal set of eigenvectors in the muscle activation space, M-modes, which were used as the elemental variables for further analysis of M-mode synergies (see section "Computation of the synergy index"). In our study, we applied the same set of M-modes, extracted from the body sway task, to the load-release task, since similar patterns of the synergy indices and M-mode compositions were found in previous studies (Klous et al. 2011; Krishnan et al. 2011, 2012).

In line with the previous literature on the muscle M-modes composition (Krishnamoorthy et al. 2003a, b; Danna-Dos-Santos et al. 2007; Krishnan et al. 2011), we classified M-modes into "ventral M-modes" (with significantly loaded ventral muscles), "dorsal M-modes" (with significantly loaded dorsal muscles), and "mixed M-modes" (which commonly had TFL and RA significantly loaded).

Within each trial of the load-release task (see later), M-mode magnitudes were calculated by multiplying the EMG_{norm} matrix (formed with 13 columns representing 13 muscles and number of rows corresponding to the number of sample analyzed) within the time window {1000 ms prior to t_0; 300 ms after t_0} by the eigenvectors.

The time of APA initiation, t_{APA}, was determined for each subject and each condition of the load-release task. The average value and standard deviation over the steady-state phase {(t_0 – 900) ms; (t_0 – 300) ms} were calculated for the ventral and dorsal M-modes. Further, t_{APA} was defined as the time when the mode magnitude differed from the average baseline value by ±2 SD. The earliest in time value, across the ventral and dorsal M-modes, was selected as t_{APA}, confirmed visually at optimal resolution.

The EMG changes during APAs were computed for each of the four conditions, for each subject and each muscle separately, by subtracting integrals of the baseline activity, estimated within the time interval {(t_0 – 900) ms; (t_0 – 300) ms} and normalized to time interval of 150 ms, from integrals calculated within {–100 ms +50 ms} with respect to t_0:

$$\int \mathrm{APA}dt = \int_{-100}^{+50} \mathrm{EMG}dt - \left(\int_{-900}^{-300} \mathrm{EMG}dt \right)/4 \quad (4)$$

Further, for brevity, we omit the "dt" in expressions including time integrals. For comparison across subjects, $\int$APA indices for each muscle were normalized by the maximal magnitude of this integral across the experimental conditions. Note that after this normalization all the $\int$APA values were within the range from +1 to −1 (as in Slijper and Latash 2000, 2004).

To quantify indices of co-activation and reciprocal activation within agonist–antagonist muscle groups at the level of M-modes, integrals of ventral and dorsal M-mode activities were calculated and analyzed (Slijper and Latash 2000, 2004; Chen et al. 2015). We used the same expression as shown in Eq. (4) to estimate the changes in M-mode magnitudes.

Subsequently, co-contraction (*C-index*) and reciprocal (*R-index*) indices were computed (Slijper and Latash 2000, 2004) within the framework of the equilibrium-point hypothesis (Feldman 1986). Since the baseline activity of the dorsal muscles was greater than that of the ventral ones (due to the initial leaning forward posture), $R = (\int \mathrm{APA}_{\mathrm{ventral}\,M\text{-modes}} - \int \mathrm{APA}_{\mathrm{dorsal}\,M\text{-modes}})$ and $C = 0$ if $\int A\mathrm{PA}_{\mathrm{ventral}\ M\text{-modes}}$ and $\int \mathrm{APA}_{\mathrm{dorsal}\ M\text{-modes}}$ had different signs; $C = \min\{|\int \mathrm{APA}_{\mathrm{ventral}\ M\text{-modes}}|; |\int \mathrm{APA}_{\mathrm{dorsal}\ M\text{-modes}}|\}$ if $\int \mathrm{APA}_{\mathrm{ventral}\ M\text{-modes}}$ and $\int \mathrm{APA}_{\mathrm{dorsal}\ M\text{-modes}}$ had the same signs.

For comparison across subjects, both R and C were normalized by the absolute highest values for each series and each subject separately.

Defining the Jacobian matrix

The objective of this step was to define the Jacobian (**J**) matrix that links small changes in M-modes (ΔM) to $\mathrm{COP_{AP}}$ displacements ($\Delta\mathrm{COP_{AP}}$), assuming linear relations between these variables (Krishnamoorthy et al. 2003b; Danna-dos-Santos et al. 2007). ΔM and $\Delta\mathrm{COP_{AP}}$ data were computed from $\mathrm{IEMG_{norm}}$ and integrated $\mathrm{COP_{AP}}$ (within 50-ms time windows) data from the body sway task. Both ΔM and $\Delta\mathrm{COP_{AP}}$ were filtered with a 5-Hz, low-pass, fourth-order, zero-lag Butterworth filter (Falaki et al. 2014, 2016). Multiple regression analysis was performed for each subject separately:

$$\Delta\mathrm{COP_{AP}} = k_1\Delta M_1 + k_2\Delta M_2 + k_3\Delta M_3 + k_4\Delta M_4 \quad (5)$$

The resulting set of coefficients from the regression were arranged in a matrix that is the **J** matrix: $\mathbf{J} = [k_1\ k_2\ k_3\ k_4]^{\mathrm{T}}$, where T is the sign of transpose. Hence, this step resulted in one **J** matrix for each subject.

Computation of the synergy index

We used the framework of the UCM hypothesis (Scholz and Schöner 1999; reviewed in Latash et al. 2007), assuming that the central nervous system manipulates a set of elemental variables (M-mode magnitudes) to stabilize a salient performance variable ($\mathrm{COP_{AP}}$ coordinate). Specifically, the inter-trial variance in the M-mode space was divided into two components, within the UCM, approximated as the null space of **J**, where the $\mathrm{COP_{AP}}$ coordinate did not change (V_{UCM}) and within the orthogonal complement to the UCM (V_{ORT}). V_{UCM} and V_{ORT} were computed within the four-dimensional M-mode space for each subject separately. The UCM was three dimensional, and the ORT subspace was one dimensional. Comparing V_{UCM} and V_{ORT}, normalized by the dimensionality of their respective subspaces, produces an index of multi-M-mode synergy (ΔV):

$$\Delta V = \frac{V_{\mathrm{UCM}} - V_{\mathrm{ORT}}}{V_{\mathrm{TOT}}} \quad (6)$$

Since V_{UCM}, $V_{\mathrm{ORT,}}$ and V_{TOT} were computed per degree of freedom, ΔV ranged between 1.33 (all variance is within the UCM) and -4 (all variance is within the ORT). For further statistical analysis, ΔV values were log-transformed (Solnik et al. 2013). For more details on the computational procedures, see earlier publications (Krishnamoorthy et al. 2003b; Danna-dos-Santos et al. 2007).

The changes in the variance indices and the synergy index (ΔV_{UCM}, ΔV_{ORT}, and $\Delta\Delta V_{\mathrm{Z}}$), were quantified as the difference between the mean magnitudes of V_{UCM}, V_{ORT}, and ΔV_{Z} over the steady state {(t_0 – 900) ms; (t_0 – 400) ms} and their respective means about the load-release time ($t_0 \pm 25$ ms).

Anticipatory synergy adjustments (ASA) were identified as a drop in the ΔV_{Z} time profile prior to t_0. The time of ASA initiation (t_{ASA}) was identified as the instant in time when ΔV_{Z} exceeded 1 SD from the average value over the steady-state phase and stayed below the average value until t_0. The t_{ASA} values were also visually confirmed by an experienced researcher.

Statistics

Data are presented in the text and figures as means and standard errors. Two-way ANOVA with repeated measures was performed with factors *Direction* (backward vs. forward) and *Condition* (known vs. unknown).

In particular, we explored how the main outcome variables such as ΔV_{UCM}, ΔV_{ORT}, $\Delta\Delta V_Z$, t_{ASA} (Hypothesis 1) and t_{APA} (Hypothesis 2A), R-indices and C-indices (Hypothesis 2B) were affected by these factors. Pairwise contrasts with Bonferroni corrections were used to explore significant effects. In all the repeated measures ANOVA, whenever the Mauchly's test of sphericity was not satisfied, the Greenhouse–Geisser correction was made. We performed a two-way MANOVA on $\int$APA values to test the effects of *Direction* and *Condition* on changes in activation of individual muscles during APAs. The level of significance was set at $p < 0.05$. All statistical analyses were performed with SPSS 21.0 (IBM Corp., Armonk, NY, USA).

Results

Identification of muscle modes and Jacobian

During the cyclical sway task, the subjects showed consistent patterns of muscle activation at the sway frequency. Typically, ventral muscles crossing different joints showed similar time patterns and proportional activation changes; the same was true for the dorsal muscles. These patterns were reflected in consistent muscle groups (M-modes, see Methods) identified in our study using the PCA with rotation and factor extraction applied to integrated indices of muscle activation. On average, the four rotated PCs (M-modes) accounted for 79.2 ± 1.6% (ranging from 78.2 to 85.9%) of the total variance.

A typical set of M-modes is presented in Table 1 with the significant loadings shown in bold. Loadings at individual muscles for the first two PCs were similar across subjects.

Indeed, one of the first two PCs showed high loading values for the dorsal muscles, while the other PC showed high loading values for the ventral muscles. The third and fourth M-modes were more variable across subjects and typically had only one or two muscles significantly loaded (typically, RA or TFL). We saw six cases of significant loadings of the same sign within an agonist–antagonist pair (co-contraction patterns) out of 44 M-modes across all subjects.

Linear regression analysis confirmed a significant linear relation between changes in the magnitudes of the M-modes and COP_{AP} shifts. All four M-modes were significant predictors of COP_{AP} shifts in all subjects ($p < 0.001$). On average, the linear regression accounted for 69 ± 2% of the total variance in COP_{AP}.

Anticipatory postural adjustments (APAs)

During the load-release trials, the subjects were instructed to lean forward before initiating the self-triggered perturbation. As a result, nonzero EMG levels (and M-modes) could be observed, particularly in the dorsal muscles, during steady-state standing. There were consistent changes in the muscle activation levels prior to the self-triggered unloading. Figure 2 shows the typical EMG time profiles for a subset of muscles in a representative subject, averaged across repeated trials with the self-triggered perturbation acting backwards (BKn) and forward (FKn) when the subject knew in advance the perturbation direction. EMG patterns under the conditions with unknown direction of perturbation (FUn and BUn) are shown in Fig. 3. Note the consistent EMG changes prior to the time of action initiation (t_0) shown in Fig. 2 with arrows. Under the Kn condition, these changes typically included reciprocal changes in the activation levels within agonist–antagonist pairs: a drop in the activation level of dorsal muscles (sometimes accompanied by an EMG burst in ventral muscles) under the BKn condition and an increase in the activation level of dorsal muscles under the FKn condition.

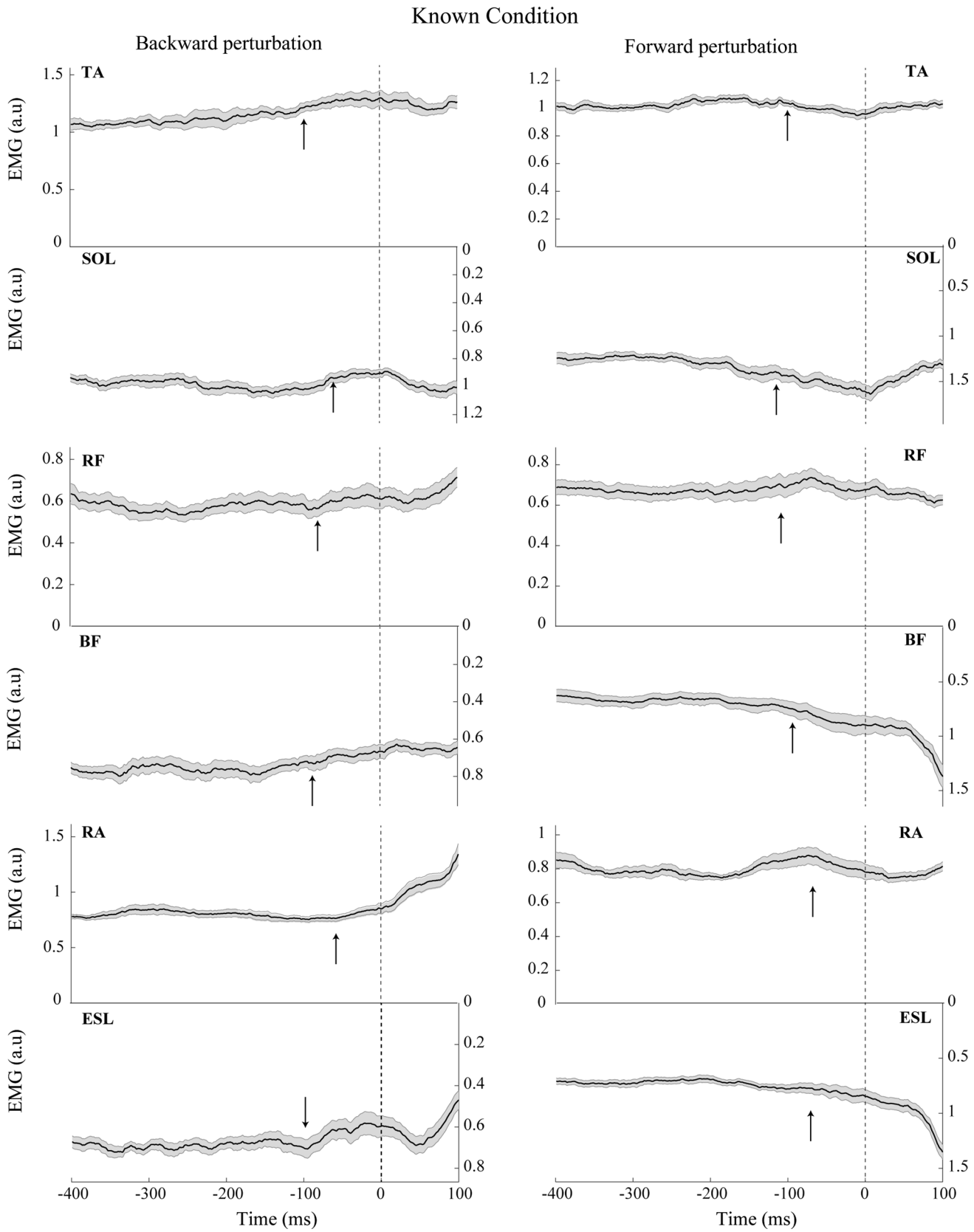
When the perturbation direction was unknown to the subject, two typical changes were observed. First, t_{APA} shifted toward the action initiation time. Averaged across subjects, t_{APA} magnitude was 117.14 ± 17.52 ms when the perturbation direction was known while t_{APA} was 60 ± 15.93 ms when the perturbation was unknown [effect of *Condition*, $F_{(1,10)} = 26.05$, $p < 0.001$]. There was no effect of perturbation direction on t_{APA} and no *Condition* × *Direction* interaction. The upper panel in Fig. 4

Table 1 Muscle loading factors for the M-modes

Muscle	M1-mode	M2-mode	M3-mode	M4-mode
TA	−0.268	**0.875**	0.054	0.180
SOL	**0.914**	−0.106	−0.029	0.017
GM	**0.921**	−0.177	−0.021	−0.067
GL	**0.918**	−0.113	−0.044	0.024
BF	**0.838**	−0.147	0.068	−0.100
ST	**0.804**	−0.400	−0.020	−0.250
VL	−0.275	**0.900**	0.031	0.118
RF	−0.134	**0.811**	0.101	0.201
VM	−0.119	**0.904**	−0.005	0.029
TFL	−0.236	0.357	0.076	**0.874**
RA	0.016	0.100	**0.990**	0.056
EST	**0.864**	−0.175	0.038	−0.237
ESL	**0.852**	−0.297	0.004	−0.209

Loading factors for the first four PCs after varimax rotation and factor extraction for a typical subject are shown. Significant loadings (greater than 0.5) are shown in bold

TA tibialis anterior, *SOL* soleus, *GM* gastrocnemius medialis, *GL* gastrocnemius lateralis, *BF* biceps femoris, *ST* semitendinosus, *RF* rectus femoris, *VL* vastus lateralis, *VM* vastus medialis, *TFL* tensor fasciae latae, *RA* rectus abdominis, *EST* thoracic erector spinae, *ESL* lumbar erector spinae


Known Condition
Backward perturbation
Forward perturbation
TA
SOL
RF
BF
RA
ESL
EMG (a.u)
Time (ms)
-400
-300
-200
-100
0
100

◂**Fig. 2** EMG time series averaged across trials by a typical subject for the backward (*left panels*) and forward perturbations (*right panels*) under the known direction of perturbation. The data for a subset of muscles are presented: tibialis anterior (TA), soleus (SOL), rectus femoris (RF), biceps femoris (BF), rectus abdominis (RA) and lumbar erector spinae (ESL) with standard error *shades*. The *vertical dashed lines* show the perturbation time ($t_0 = 0$). *Arrows* show the onset of APAs (t_{APA}). Note the reciprocal activations of muscles before the perturbation onset. EMG activity is in normalized units. EMG signals for SOL, BF, and ESL are inverted for better visualization

shows the averages and standard error values for t_{APA} across the four conditions.

In addition, under the Un conditions, subjects frequently showed unidirectional changes in the EMG levels within agonist–antagonist pairs during APAs. Note the increase in the activation level of both dorsal (SOL, BF and ESL) and ventral (TA, RF, and RA) muscles prior to the perturbation time ($t_0 = 0$) in Fig. 3.

Table 2 presents the indices of APA activity ($\int$APA) values for all muscles averaged across subjects with standard errors for each of the four conditions. MANOVA showed a significant *Condition* × *Direction* interaction [$F_{(13,28)} = 3.140$, $p < 0.01$; Wilks' $\Lambda = 0.407$] without other effects (effect of *Direction* was close to significance, $p = 0.081$). ANOVAs performed on individual muscle indices confirmed significant *Condition* × *Direction* interactions for TA, SOL, GM, GL, BF, ST, EST, and ESL ($p < 0.05$). *Direction* effects were significant for SOL, GM, ST, EST, and ESL, while *Condition* effects were significant for SOL, RF, EST, and ESL.

In our further analysis, we reduced the changes in individual muscle activations to two indices, the *C*-index and *R*-index, computed based on the M-mode values (see Methods) to quantify parallel versus reciprocal changes in the EMG signals. These values are also presented in Table 2 (two bottom rows) and in Fig. 4 (middle and lower panels). Note the negative *R*-values for the BKn condition and positive values for the FKn condition. In contrast, for the BUn and FUn conditions, both values were positive and smaller in magnitude. These differences were reflected in significant effects of both *Condition* $F_{(1,10)} = 87.77$, $p < 0.001$ and *Direction* $F_{(1,10)} = 16.7$, $p < 0.01$, and a *Condition* × *Direction* interaction ($F_{(1,10)} = 78.37$, $p < 0.001$), with respect to the *R*-index. The interaction reflected the fact that *Direction* had a significant effect on the R-index when the subjects knew the perturbation direction ($p < 0.001$), while this was not true when the subjects did not know the perturbation direction. The *C*-index increased when the subjects had no prior knowledge about the direction of perturbation ($F_{(1,10)} = 9.1$, $p < 0.05$), without other effects.

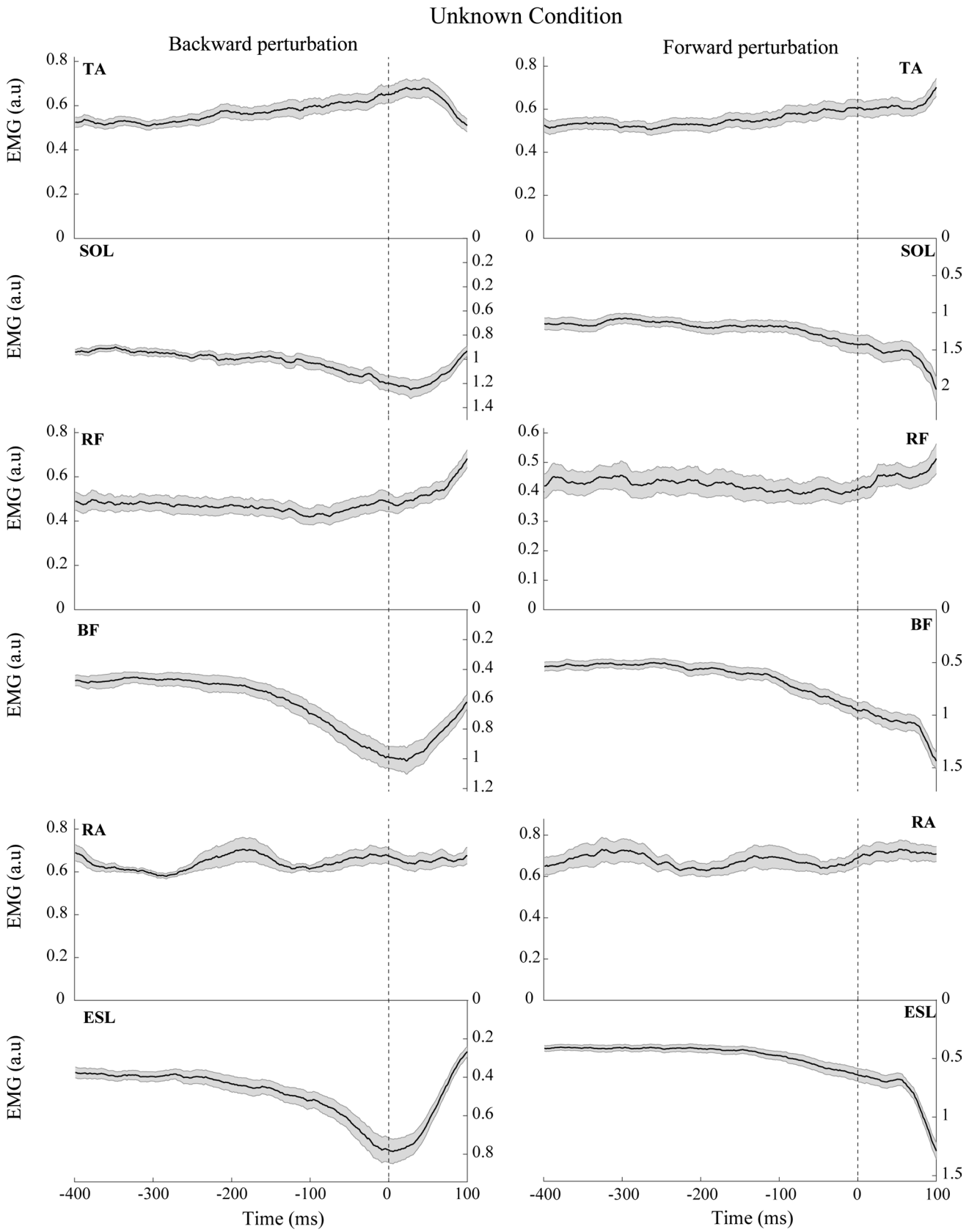
Analysis of multi-M-mode synergies

We used the framework of the UCM hypothesis to quantify multi-M-mode synergies stabilizing the COP_{AP} trajectory. For this purpose, two components of variance in the M-mode space were quantified, V_{UCM} and V_{ORT} (see "Methods"). The time profiles of the averaged across-subjects values of V_{UCM} and V_{ORT}, quantified per degree of freedom, are shown in Fig. 5 for each of the four conditions. Note the increase in V_{ORT} that could be seen about 200 ms prior to the perturbation time (t_0) across all conditions (shown with arrows in Fig. 5). These changes caused a drop in the synergy index (z-transformed, ΔV_Z), which we address as ASA. The time profiles of the synergy index during ASAs are illustrated in Fig. 6. Averaged across-subjects timing of ASAs with error bars is presented in Fig. 7 for the four conditions. Note that the time of ASA initiation (t_{ASA}, shown with arrows in Fig. 6) was seen prior to the initiation of APA (t_{APA}) across all four conditions. The averaged values of the changes in V_{UCM}, V_{ORT}, and ΔV_Z during ASAs (ΔV_{UCM}, ΔV_{ORT}, and $\Delta\Delta V_Z$, respectively) within each series are presented in Table 3.

During steady state, there were no significant effects of *Condition* and *Direction* on any of the three variance indices, V_{UCM}, V_{ORT}, and ΔV_Z (these values are presented in Table 3). ASA characteristics, the time of ASA initiation (t_{ASA}), and magnitude of the drop in the synergy index ($\Delta\Delta V_Z$) also showed no significant effects of these two factors. Figure 7 depicts t_{ASA} data timing averaged across subjects for the four conditions. When the subject knew the perturbation direction in advance, t_{ASA} was 176.82 ± 13.81 ms (BKn) and 170.64 ± 8.32 ms (FKn), as shown in Fig. 7. When the perturbation direction was unknown, t_{ASA} was 163.00 ± 18.05 and 158.82 ± 22.17 ms for the BUn and FUn series, respectively.

Discussion

In "Introduction", we formulated contrasting predictions with respect to possible changes in anticipatory postural adjustments (APAs) and anticipatory synergy adjustments (ASAs) when the subjects become unable to predict direction of a self-triggered perturbation. Our observations provided support for all the specific hypotheses. In particular, we saw no significant changes in the two characteristics of ASAs (t_{ASA} and $\Delta\Delta V_Z$) between conditions with predictable and unpredictable direction of perturbations in support of Hypothesis 1. In contrast, there were significant changes in APA characteristics. In particular, as predicted by Hypothesis 2A, APAs became delayed under the conditions


Unknown Condition
Backward perturbation
Forward perturbation
TA
SOL
RF
BF
RA
ESL
EMG (a.u)
Time (ms)
-400
-300
-200
-100
0
100

◂**Fig. 3** EMG time series averaged across trials by a typical subject for the backward (*left panels*) and forward perturbations (*right panels*) under the unknown direction of perturbation. The data for a subset of muscles are presented. For abbreviations, see Fig. 2. Note the unidirectional changes in muscle activation levels before the perturbation onset. EMG activity is in normalized units. EMG signals for SOL, BF, and ESL are inverted for better visualization

with unpredictable directions of perturbations. In addition, the typical reciprocal APA pattern observed when the subjects knew the direction of the perturbation in advance switched to a more pronounced co-contraction pattern in support of Hypothesis 2B. Overall, these results show that feed-forward control of vertical posture has two distinct components that depend differently on prior knowledge about perturbation direction. We discuss implications of these results for the recently proposed hierarchical scheme of the synergic control of motor tasks.

Multi-muscle synergies: definitions and role in motor control

There is no consensus in the movement science literature on the meaning of *synergy* (reviewed in Latash and Zatsiorsky 2016). In clinical studies, this word commonly means a stereotypical pattern of muscle activation interfering with purposeful voluntary movements seen commonly after stroke (De Wald et al. 1995). More commonly, *synergy* means a group of variables with proportional involvement into an action over time and/or over changes in the action characteristics. In particular, synergies were defined as proportional changes in joint displacements, forces, and muscle activations (D'Avella et al. 2003; Jerde et al. 2003; Braido and Zhang 2004; Zatsiorsky et al. 2004; Tresch et al. 2006). This definition emphasizes a reduction in the number of hypothetical variables manipulated by the controller as compared to the number of variables at the level of effectors. As such, synergies are supposed to contribute to dealing with the problem of motor redundancy.

A different definition has been formulated and developed recently based on the principle of motor abundance (Gelfand and Latash 1998; Latash 2012). This principle views the apparent excess of elemental variables at the level of effectors not as a source of computational problems for the neural controller but as a rich apparatus that can be used to provide stability of various performance variables in a task-specific way (cf. Schöner 1995). Synergies are defined in a space of elemental variables as neural organizations of the elemental variables with the purpose to stabilize task-specific salient variables.

Defining elemental variables is a nontrivial step in the definition and analysis of specific synergies (reviewed in Latash 2008). In particular, during whole-body multi-muscle tasks, stable muscle groups with proportional scaling of

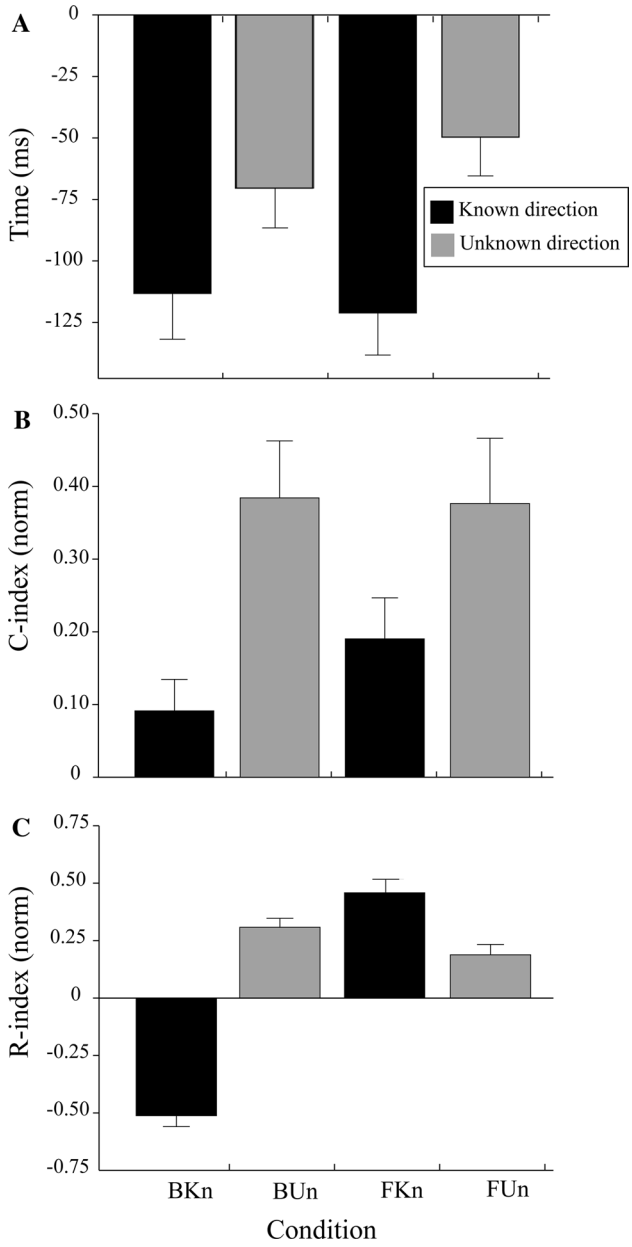


Fig. 4 Averaged across-subjects characteristics of anticipatory postural adjustments (APAs) are shown with *standard error bars*: **a** APA timing, t_{APA}; **b** *C*-index and **c** *R*-index. Note the significant delay in APAs (*panel A*) and the reorganization of APAs (*panels B* and *C*) when the perturbation direction was unknown (BUn and FUn). *BKn* backward perturbation with known direction; *FKn* forward perturbation with known direction; *BUn* backward perturbation with unknown direction; *FUn* forward perturbation with unknown direction

muscle activations have been viewed as elemental variables (M-modes, Krishnamoorthy et al. 2003a); note that such groups are called synergies according to the second of the mentioned definitions.

According to the principle of motor abundance, the problem of motor redundancy is apparent, not real: The

Table 2 Characteristics of APAs

	BKn	FKn	BUn	FUn
TA	−0.008 ± 0.011	0.104 ± 0.032	0.114 ± 0.042	0.071 ± 0.023
SOL	−0.067 ± 0.024	0.1 ± 0.027	0.107 ± 0.03	0.056 ± 0.023
GM	−0.184 ± 0.059	0.133 ± 0.033	0.094 ± 0.061	0.009 ± 0.052
GL	−0.117 ± 0.07	0.189 ± 0.085	0.177 ± 0.073	0.059 ± 0.021
BF	−0.104 ± 0.027	0.119 ± 0.041	0.072 ± 0.047	0.007 ± 0.045
ST	−0.095 ± 0.029	0.147 ± 0.041	0.099 ± 0.045	0.058 ± 0.038
VL	0.018 ± 0.008	0.007 ± 0.009	0.01 ± 0.008	0.012 ± 0.012
RF	0.014 ± 0.009	−0.003 ± 0.011	−0.008 ± 0.01	−0.019 ± 0.007
VM	0.003 ± 0.006	−0.005 ± 0.009	0.022 ± 0.01	−0.002 ± 0.01
TFL	0.002 ± 0.006	0.033 ± 0.018	0.033 ± 0.021	0.007 ± 0.008
RA	0.003 ± 0.011	0.001 ± 0.011	0.002 ± 0.007	0.003 ± 0.006
EST	−0.113 ± 0.031	0.135 ± 0.024	0.102 ± 0.028	0.053 ± 0.026
ESL	−0.098 ± 0.021	0.128 ± 0.028	0.092 ± 0.024	0.034 ± 0.02
R-index	−1.024 ± 0.095	0.916 ± 0.118	0.616 ± 0.078	0.551 ± 0.151
C-index	0.091 ± 0.043	0.19 ± 0.056	0.384 ± 0.078	0.377 ± 0.09

The top rows show the ∫APA indices for individual muscles; the two bottom rows show the reciprocal (R-index) and co-activation (C-index) indices (mean ± SE). ∫APAs, R-, and C-indices are in normalized units

BKn backward perturbation with known direction, *FKn* forward perturbation with known direction, *BUn* backward perturbation with unknown direction, *FUn* forward perturbation with unknown direction. See Table 1 for the abbreviation of muscles

apparently redundant degrees of freedom are not eliminated but used in each trial in a flexible manner to ensure stable performance with respect to salient performance variables. The redundancy–abundance issue is discussed in detail in several recent reviews and books (Latash 2010, 2016; Latash and Zatsiorsky 2016). Since we accept the principle of abundance, the arrangement of muscles into M-modes is not a step toward solving the problem of redundancy. Within the idea of movement control with changes in referent body configurations (RC hypothesis, Feldman 2015), M-modes may be viewed as reflections of elemental changes in the body RC, which are used as the basis for a variety of whole-body actions (Latash 2010). This idea is indirectly supported by the analysis of whole-body actions as combinations of *eigenmovements* (Alexandrov et al. 2001). An eigenmovement is movement along a new coordinate, which represents a linear combination of joint rotations; this coordinate is selected to ensure that movement along this coordinate depends only on the moment of force vector along the same coordinate and not on moments along other eigenmovements. The patterns of eigenmovements, analyzed both theoretically and experimentally, are compatible with changes in body configuration similar to those addressed as ankle strategy and hip strategy, as well as with the typical composition of M-modes (Horak and Nashner 1986; Robert et al. 2008).

Note that the number of eigenmovements is not smaller than the number of joint rotations (both equal three in the studies of Alexandrov et al. 2001). This is an example of a more general idea that task-specific selection of a basis is not ruled by the idea of reducing the number of variables but by a deeper idea of ensuring an optimal basis given the control structure and task specificity. Such a change of the system of coordinates may reflect the nature of control with RCs. It may also be driven by the desire to use local control, i.e., changing an elemental variable only when that particular variable is perturbed. Using such control variables may be beneficial for implementing simple rule-based (algorithmic) control of the body able to ensure stability in conditions of unpredictable perturbations such as, for example, when slipping during walking on ice (Akulin et al. 2015).

Feed-forward control of vertical posture

Mechanisms of feed-forward control of vertical posture were predicted by Bernstein (1947) and described for the first time about 50 years ago (Belenkiy et al. 1967). Since those pioneering works, anticipatory postural adjustments have been studies vigorously in both young, healthy persons and populations with impaired postural control (reviewed in Massion 1992, 1998). In particular, APA characteristics have been shown to depend on several factors such as properties of the perturbation (its magnitude, point of application, and direction), properties of action associated with the perturbation, time pressure, and stability of

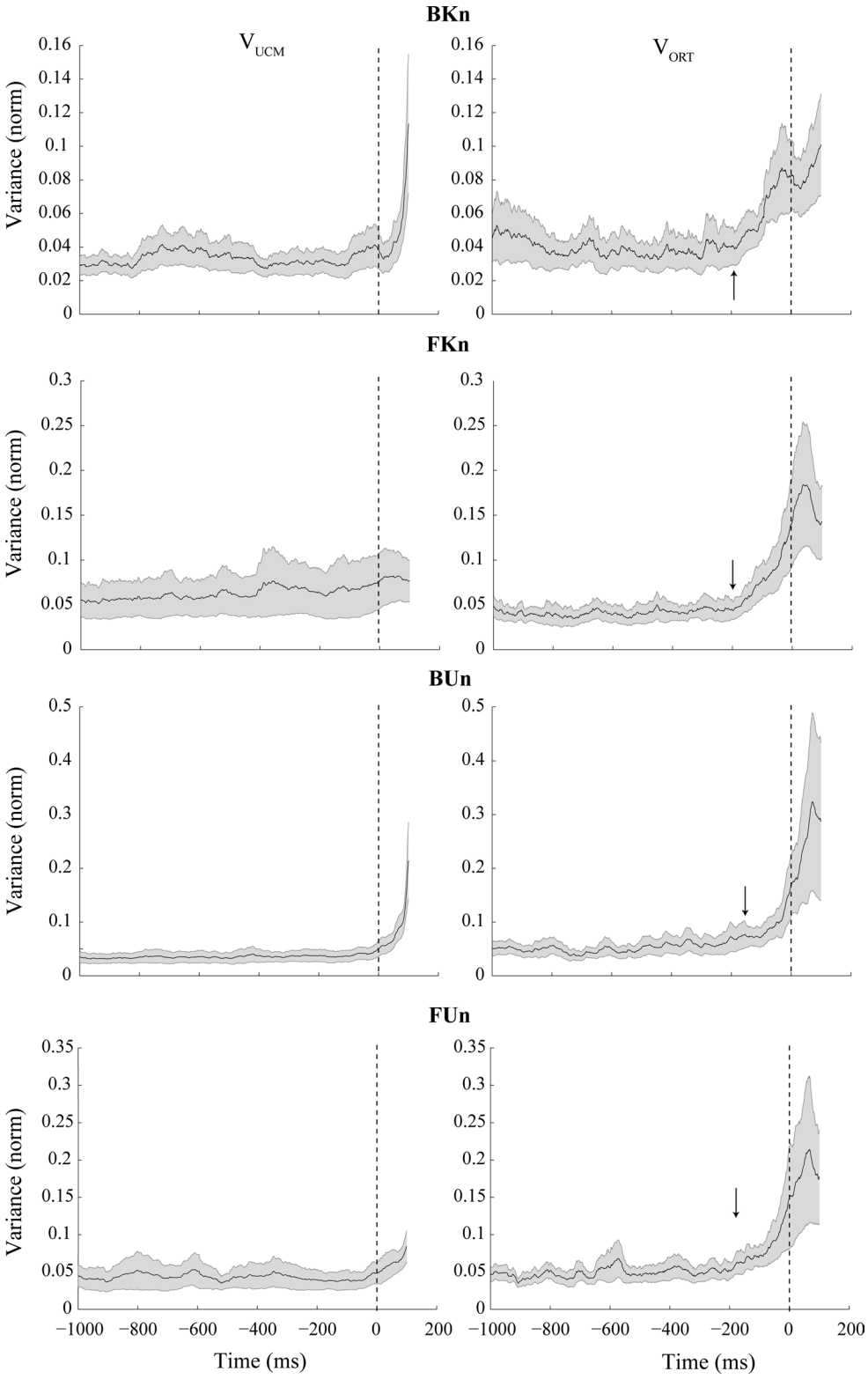


Fig. 5 Time profiles of the two components of inter-trial variance, V_{UCM} (*right plots*) and V_{ORT} (*left plot*), averaged across subjects for each condition. The *vertical dashed line* corresponds to the onset of the perturbation ($t_0 = 0$). Note the similar time profile of V_{UCM} and V_{ORT} across the four conditions and the increase of V_{ORT} before t_0 shown by *arrows*. For abbreviations, see the caption for Fig. 4

the initial posture (reviewed in Aruin 2002; Latash and Hadders-Algra 2008). The purpose of APAs has been typically assumed as the generation of forces and moments directed against those expected from the perturbation (Cordo and Nashner 1982; Bouisset and Zattara 1987; Ramos and Stark 1990). Note that, according to this hypothesis, APAs make functional sense only if the direction of forces/moments associated with a perturbation is

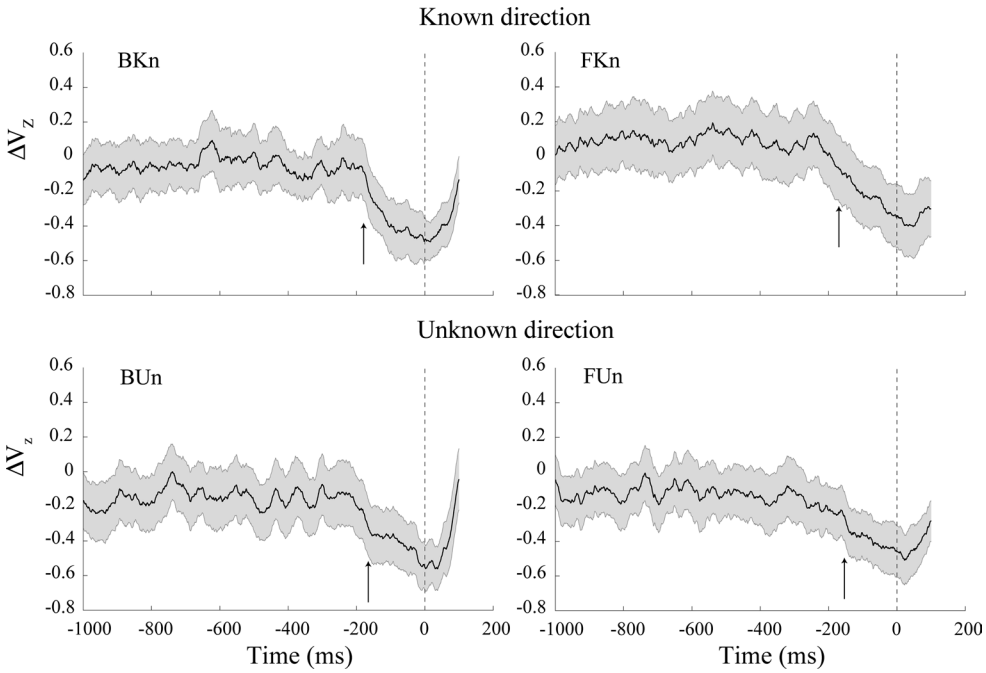


Fig. 6 Time profiles of the synergy index (ΔV_Z), averaged across subjects for the four conditions. The *vertical dashed line* shows the perturbation time ($t_0 = 0$). The onset of ASAs initiation (t_{ASA}) is shown by *arrows*. Note the similar ΔV_Z values and time profiles across the four conditions. For abbreviations, see the caption for Fig. 4

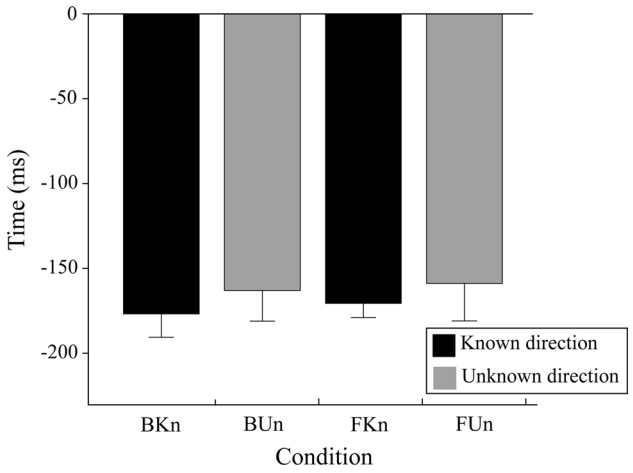


Fig. 7 Characteristics of anticipatory synergy adjustments (ASAs) averaged across participants with *standard error bars* are shown for the four conditions. Note that ASAs occurred before APAs (compared to the data in Fig. 4). For abbreviations, see the caption for Fig. 4

known to the subject in advance. In our experiment, when this was not the case, APAs had to disappear or rearrange.

When properties of a perturbation are not known to the subject in advance, APAs show modifications compared to typical patterns seen when the subjects do not have to guess. In particular, when magnitude of a perturbation is unknown, subjects tend to generate APAs appropriate for the larger load (Aimola et al. 2011) or scale them with respect to the load experienced in the immediately preceding trial (Toussaint et al. 1998). To our knowledge, no previous studies explored APAs in conditions when *direction* of perturbation was unknown to the subject.

We observed two significant differences between the conditions with predictable and unpredictable perturbation directions: delayed APAs and prevalence of co-contraction patterns in agonist–antagonist muscle groups. Both changes may be seen as driven by safety considerations. Note that APAs have been shown to reverse their pattern and act in the direction of a self-triggered perturbation if their effects on COP shifts led the subject to a safer posture (Hirschfeld and Forssberg 1991; Krishnamoorthy and Latash 2005). In our study, APAs during the load manipulations were not vital for keeping vertical posture. COP shifts observed during APAs are relatively small in magnitude (on the order of a few mm; Bouisset and Zattara 1987; Massion 1992) as compared to the distance from the edge of support. Indeed, when similar tasks are performed in the simple reaction time paradigm, APAs are initiated closer to the moment of action initiation, and subjects have no problems keeping balance (Lee et al. 1987; DeWolf et al. 1998). However, even in the mentioned simple reaction time tasks, perturbation direction was always known to the subjects in advance.

Another strategy of APA adjustment in conditions viewed by the subjects as uncertain and/or otherwise difficult is to switch from the typical reciprocal pattern of muscle activation (optimal from the point of view of generating forces and moments) to an alternative pattern of co-contracting muscles. Note that co-contraction patterns during APAs have been described in the healthy elderly (Woollacott et al. 1988), persons with atypical development (Aruin

Table 3 Changes in the variance indices during ASAs

	BKn	FKn	BUn	FUn
ΔV_{UCM}	-0.003 ± 0.005	-0.018 ± 0.011	-0.016 ± 0.008	-0.005 ± 0.005
ΔV_{ORT}	-0.043 ± 0.012	-0.105 ± 0.044	-0.112 ± 0.048	-0.100 ± 0.053
$\Delta\Delta V_Z$	0.44 ± 0.04	0.46 ± 0.04	0.39 ± 0.07	0.38 ± 0.06

The means across subjects with standard error values are presented for the four conditions. ΔV_{UCM}, ΔV_{ORT}, $\Delta\Delta V_Z$ are in normalized units. For abbreviations, see Table 2

and Almeida 1997), patients with neurological disorders (Asaka and Wang 2011), as well as in young, healthy persons performing tasks associated with a difficult postural component (Gantchev and Dimitrova 1996). In some of those conditions, even the organization of muscle into M-modes showed a switch from the typical patterns (e.g., similar to those illustrated in Table 1) to agonist–antagonist muscles represented in the same M-mode with loading factors of the same sign (co-contraction patterns, Danna-dos-Santos et al. 2008; Asaka and Wang 2011).

The significant changes in APA characteristics with predictability of the perturbation direction in our study stand in contrast to no changes in characteristics of the second feed-forward adjustment, ASAs. According to previous studies, the main purpose of ASAs is to reduce stability of a variable that the subject plans to change quickly (reviewed in Latash and Zatsiorsky 2016). Indeed, producing a quick change in a variable stabilized by a synergy requires overcoming one's own synergy. This is true independently of the planned direction of change in that variable. Indeed, an earlier study with known and unknown direction of changes in the force pulse produced by a set of fingers showed no dependence of ASAs on predictability of the force pulse direction (Zhou et al. 2013).

To use a more intuitive example, when a goalkeeper gets ready for a penalty kick, he or she never stands perfectly quietly, but shows substantial body sway, which may help to initiate the upcoming action independently of the direction of the kick. In clinical studies, a reduction in ASAs was seen in patients with Parkinson's disease who, according to the clinical examination, showed no signs of postural instability (Falaki et al. 2016). It is possible that the inability to destabilize a variable with ASAs contributed to the well-known episodes of freezing, which represent one of the most disabling factors in these patients.

Feed-forward adjustments within the hierarchical control of multi-muscle systems

The notion of synergy fits naturally the hierarchical scheme for the control of movements developed recently (Latash 2014, 2016). This scheme is based on the idea of control with referent coordinates (RCs) for salient variables at each level of the hierarchy. At the highest level, a low-dimensional set of spatial RCs is used for the task-specific variables. Further, these variables undergo a chain of few-to-many transformations resulting in RCs at the level of elemental variables such as referent body configurations (reflected in M-modes), individual joint rotations, and ultimately in RCs for the individual muscles. RCs at this latter level are equivalent to the values of the threshold of the tonic stretch reflex as in the classical equilibrium-point hypothesis (Feldman 1966, 1986). Back-coupling loops ensure stability of values (time profiles) of RCs at higher levels by covaried adjustments of RCs at lower levels (e.g., as in Latash et al. 2005).

This scheme involves two types of neural variables that define target values (trajectories) for the salient variables and their stability properties, respectively. The former (NV1) are associated with the RCs at the task level, while the latter (NV2) may be associated with the gain matrix describing the back-coupling loops. The existence of these two classes of neural variables is supported by observations of unchanged performance with changes in synergy indices (e.g., during the ASAs, Olafsdottir et al. 2005; Klous et al. 2011), by changes in performance without changes in synergy indices (Friedman et al. 2009), as well as by observations in neurological patients. In particular, patients with subcortical disorders, even at the earliest stages, typically demonstrate only slightly changed performance accompanied by significant changes in the synergy index (reviewed in Latash and Huang 2015). In contrast, patients after stroke sometimes demonstrate grossly changed performance with no changes in the synergy index (Reisman and Scholz 2003; Jo et al. 2016). These findings, taken together with the outcome of our study, are promising to increase the knowledge of salient features of the neural control of movement with potential implications for rehabilitation strategies. The theoretical framework of the concept of synergy and the hierarchical scheme for the control of movements need to be translated into rehabilitation science as they may help to develop new treatment strategies and approaches (reviewed in Piscitelli 2016).

Feed-forward control of posture may be associated with changes in each group of the assumed neural variables. In particular, a change in NV1 in preparation to an action leads to APAs. In contrast, a change in NV2 leads to ASAs. Several earlier studies have provided evidence for the different timing of ASAs and APAs in postural tasks (Klous et al.

2011; Krishnan et al. 2011, 2012). ASAs emerge about 200–300 ms prior to the action initiation, while APAs start about 100 ms prior to the action initiation. This observation, by itself, also supports the idea of two groups of variables, NV1 and NV2, involved in the feed-forward control of tasks with postural components. Our results provide additional support for this scheme by showing decoupled changes in ASAs and APAs with changes in predictability of the perturbations.

A number of studies have provided evidence for parallel changes in features of ASAs and APAs. These include the delays in both adjustments under the simple reaction time instruction (De Wolf et al. 1998; Olafsdottir et al. 2005), delayed and reduced adjustments in the healthy elderly (Woollacott et al. 1988; Olafsdottir et al. 2007), and in certain patient groups (Bazalgette et al. 1987; Park et al. 2012; Jo et al. 2016). Since the neural processes leading to these two types of feed-forward adjustments are independent, at least hypothetically, the mentioned observations suggest that our understanding of the feed-forward processes is incomplete. There are likely higher-order processes involved in feed-forward control that are reflected in both ASAs and APAs, possibly related to a more general ability to anticipate forthcoming events (reviewed in Nadin 2015).

Concluding comments

We have shown, for the first time, that two types of feed-forward control, reflected in APAs and ASAs, during motor tasks performed by standing persons show qualitatively different adjustments with changes in predictability of the direction of perturbation. These observations underscore the complexity of the feed-forward postural control, which involves separate changes in salient performance variables (such as COP coordinate) and in their stability properties. Preserved ASAs in conditions with unpredictable perturbation direction are functionally important because they destabilize the COP coordinate and facilitate later, corrective reactions to the actual perturbation. Note that the delayed and less efficient APAs make the corrective postural adjustments more important for keeping balance (cf. Santos et al. 2010; Kanekar and Aruin 2014).

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