Published in final edited form as:

Exp Brain Res. 2008 January ; 184(3): 323–338. doi:10.1007/s00221-007-1101-2.

Learning Effects on Muscle Modes and Multi-Mode Postural Synergies

Tadayoshi Asaka¹⁾, Yun Wang²⁾, Junko Fukushima¹⁾, and Mark L. Latash³⁾

¹⁾Department of Health Sciences, School of Medicine, Hokkaido University

²⁾Department of Health and Science, Graduate School of Education, Hiroshima University

³⁾Department of Kinesiology, The Pennsylvania State University

Abstract

We used the framework of the uncontrolled manifold hypothesis to explore the effects of practice on the composition of muscle groups (M-modes) and multi-M-mode synergies stabilizing the location of the center of pressure (COP). In particular, we tested a hypothesis that practice could lead to a transition from co-contraction muscle activation patterns to reciprocal patterns. We also tested a hypothesis that new sets of M-modes would form stronger synergies stabilizing COP location. Subjects practiced load release tasks for five days while standing on a board with a narrow support surface (“unstable board”). Their M-modes and indices of multi-M-mode synergies were computed during standing without instability and during standing on an unstable board before practice, in the middle of practice, and at the end of practice. During standing without instability, subjects showed two consistent M-modes uniting dorsal and ventral muscles of the body respectively (reciprocal modes). While standing on an unstable board, prior to practice, subjects commonly showed M-modes uniting muscle pairs with opposing actions at major leg joints - co-contraction modes. Such sets of M-modes failed to stabilize the COP location in the anterior-posterior direction. Practice led to better task performance reflected in fewer incidences of lost balance. This was accompanied by a drop in the occurrence of co-contraction M-modes and the emergence of multi-mode synergies stabilizing the COP location. We conclude that the central nervous system uses flexible sets of elemental variables (modes) to ensure stable trajectories of important performance variables (such as COP location). Practice can lead to adjustments in both the composition of M-modes and M-mode co-variation patterns resulting in stronger synergies stabilizing COP location.

Keywords

Posture; practice; muscle mode; synergy; electromyogram; human

Introduction

Maintaining vertical posture in the field of gravity has been one of the intensively studied motor tasks - an example of the problem of motor redundancy (Bernstein 1967). The coordination of the many muscles involved in standing has been viewed as an example of muscle synergies, large groups of muscles united by a common motor goal (Bernstein 1967; Ivanenko et al. 2004, 2005; Ting and Macpherson 2005).

Recently, the notion of muscle synergies has been operationally defined within the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999; Latash et al. 2002; Krishnamoorthy et al. 2003a). Within this hypothesis, a neural controller acts in a space of elemental variables and organizes co-variation among those variables to stabilize a value or a time profile of an important performance variable. Synergies have been defined as neural organizations that ensure stabilization of performance variables by co-variation of elemental variables. In postural tasks, performance variables have been commonly associated with coordinates of the center of pressure (COP), the point of application of the resultant ground reaction force acting on the body (Krishnamoorthy et al. 2003a,b; Wang et al. 2005, 2006; Danna-Dos-Santos et al. 2007). However, the issue of elemental variables has been more complicated.

The apparatus of the UCM hypothesis is built on analysis of co-variation among elemental variables. As such, it assumes that co-variation is absent in the absence of a particular control strategy. In other words, the controller is assumed to be able to vary elemental variables one at a time. This is not true with respect to activation levels of individual muscles that frequently show patterns of co-variation across wide variations of tasks and conditions (Krishnamoorthy et al. 2003a; Danna-Dos-Santos et al. 2007). In several earlier studies of postural tasks, elemental variables have been associated with muscle groups within which muscle activation levels scale in parallel with variations of task characteristics; these have been called muscle modes or M-modes (Krishnamoorthy et al. 2003a,b; Wang et al. 2005, 2006; Danna-Dos-Santos et al. 2007). All those studies explored issues of stabilization of COP trajectories within the space of M-modes. M-modes were defined in those studies using principal component analysis with factor extraction. Other matrix factorization techniques have been used to identify such muscle groups (d'Avella et al. 2003; Ivanenko et al. 2004; Weiss and Flanders 2004; Ting and Macpherson 2005; Tresch et al. 2006), but the authors of those studies addressed such groups as “synergies”, while we view them as elemental variables forming a space, within which synergies are organized.

Within the general scheme of synergies originally introduced by Gelfand and Tsetlin (1966), elemental variables are themselves synergies at a different level of analysis. If M-modes are indeed synergies, they may be expected to show flexibility with task variations and with practice. One of the earlier studies described “atypical” M-modes in subjects who performed load release and quick arm movement tasks while standing on a board with a decreased area of support (Krishnamoorthy et al. 2004). Those modes corresponded to parallel changes in the activation levels of muscles with opposing actions at major joints of the main axis of the body. They were termed “co-contraction modes” in contrast to the more typical “reciprocal modes” when dorsal or ventral muscles across several joints show parallel scaling of their activation levels. Unfortunately, the aforementioned earlier study did not compare M-modes in the same subjects across conditions with different postural stability.

In the present study, we have tried to answer the following three questions. Can muscle groups re-organize in the same persons with a change in postural stability conditions? Can muscle groups re-organize with practice? Can re-organization of muscle modes with practice lead to stronger multi-muscle (multi-M-mode) synergies stabilizing COP shifts? We hypothesized that all three questions would be answered affirmatively.

Methods

General Design

To address the first question formulated in the Introduction, we compared muscle modes between two conditions, standing directly on the force plate and standing on a board with a decreased dimension of support in the anterior-posterior (AP) direction - Board-1. We used a

voluntary sway (VS) task in the AP direction under the stable condition because it allows the identification of muscle modes based on a relatively small number of trials (Wang et al. 2006; Danna-Dos-Santos 2007). The voluntary sway task was impossible to be performed while standing on the unstable board. Hence, we used a load release (LR) task, as in a number of earlier studies (Krishnamoorthy et al. 2003a, b, 2004). Note that the composition of the modes was similar across all the cited studies and methods of their identification. Further, the data from the same tasks were used to identify relations between small changes in the magnitudes of the modes and COP shifts (the Jacobian).

To find answers to the second and third questions, we asked the subjects to practice for five consecutive days the load release task and a quick arm movement task while standing on two challenging boards (Boards A and B). The five-day training protocol was selected as a trade-off between inducing substantial changes in the muscle modes and synergies and having a reasonably small number of laboratory visits. The subjects were tested using the load release task while standing on Board-1 in the middle and at the end of practice. This was done to explore whether the composition of modes could change with practice. To avoid circular logic, we used another task, the quick arm movement (AM) task and analysis within the UCM, to quantify multi-M-mode synergies stabilizing the COP shifts. The selection of the three tasks (VS, LR, and AM) was based on our earlier experience and on practical considerations such the total number of trials a subject could possibly perform within a session without fatigue.

Subjects

Eight healthy subjects, four males and four females, mean weight 57.3 kg (± 8.9 SD), mean height 165.1 cm (± 7.0 SD) and mean age 20.7 years (± 1.2 SD), without any known neurological or motor disorder, participated in the experiment. All subjects were right foot dominant. The tests used to determine the dominant foot included kicking a ball, stepping up on a stair, and leading off in the long jump. All the subjects gave informed consent based on the procedures approved by the ethics committee of Hokkaido University School of Medicine.

Apparatus

A force platform (Kistler, Type 9286A, Switzerland) was used to record the shear force (F_y) in the anterior-posterior (AP) direction and the vertical component of the reaction force (F_z). A 17-in computer monitor was placed about 2 m away from the subject, at the eye level. The monitor showed a horizontal line and a cursor corresponding to the instantaneous position of the difference (ΔF_z) between the vertical force components anterior to the subject ($F_{z1} + F_{z2}$) and the posterior components of the vertical force ($F_{z3} + F_{z4}$) (Fig.1). The purpose of this feedback was to help the subject to adjust the COP location in the middle of the narrow base of support under the unstable conditions (describe later). The horizontal line corresponded to $\Delta F_z = 0$.

Disposable self-adhesive electrodes (Ambu Corporation) were used to record the surface muscle activity (EMG) of the following muscles: tibialis anterior (TA), lateral head of gastrocnemius (GL), medial head of gastrocnemius (GM), soleus (SOL), rectus femoris (RF), vastus lateralis (VL), biceps femoris (BF), semitendinosus (ST), rectus abdominis (RA), and erector spinae (ES). The electrodes were placed on the left side of the subject's body over the muscle bellies, with their centers 3 cm apart. In addition, a reference electrode was attached to the lateral aspect of the fibula.

The EMG signals were transmitted wirelessly, then amplified ($\times 2000$) and band pass filtered (30-100 Hz). All the signals were digitized at the sampling frequency of 1000 Hz with a 12-bit resolution. A personal computer (HP Workstation 2.8 GHz) was used to control the experiment and collect the data using the customized software based on the LabView-8 package

(National Instruments, Austin, TX, USA). A uni-directional accelerometer (Nihonkoden, TA-512G) was taped on the load (the LR task) or the dorsal aspect of the subject's right hand, just under the center of the wrist joint (the AM task). The axis of sensitivity of the accelerometer was directed along the motion of the load or arm; signals from the accelerometer were primarily used for trial alignment.

The subjects stood barefoot on the force platform ("stable condition") or on a specially constructed wooden board (400×400×20 mm; "unstable condition"). This board, Board-1, was fitted with a narrow beam on the undersurface (50 mm wide, 60 mm high, and 400 mm long; see Figure 1). The board was placed over the force platform such that its narrow dimension was in the AP direction. The center of the supporting beam was adjusted to coincide with the center of the force platform. Prior to each trial, the subjects were required to adjust the posture to make sure that the cursor showing the COP location (estimated as the difference in the vertical forces, ΔF_z) was on the horizontal target line shown on the monitor. In addition, the subjects were reminded to keep the body upright.

Experimental tasks

Three types of tasks were used based on a previous study (Krishnamoorthy et al. 2004). Two tasks were associated with anticipatory postural adjustments (APAs) and involved shifts of the center of pressure in the anterior-posterior direction (COP_{AP}) as an implicit component. The first task required the subject to release the load from extended arms (Aruin and Latash 1996). Loads of different weight could be used in different trials. The second task required the subject to perform fast bilateral arm movements (Belen'kii et al. 1967).

Load release at the back (LR)—The subjects stood upright on an unstable board with his/her feet side-by-side, at about hip width. The subjects were asked to hold a load suspended behind the body through the pulley system by pressing with the hands of the extended arms on the two round ends of the light horizontal handle (Fig.1). The upward acting load was used to avoid excessive fatigue associated with holding the combined weight of the arms and the load. The load mass ranged from 2 kg to 5 kg, in increments of 0.5 kg. Subjects were instructed to release the load in a self-paced manner with a quick, large amplitude, bilateral shoulder abduction movement (Shiratori and Aruin 2006). The total of 63 trials were performed; those included nine repetitions (presented as a block) of releasing each of the seven loads in a balanced order. If a subject lost balance prior to and/or after releasing the load, that trial was discarded and repeated. Loss of balance was obvious because the board tilted and its edge hit the platform.

Arm movement backwards (AM)—The subjects stood upright with his/her feet side-by-side, at about hip width, and the arms hanging loosely by the sides; the COP location was the same as in the LR trials. The subjects were asked to perform a fast, bilateral arm extension movement. This action leads to an initial COP shift forward, in the same direction as in the LR task. The subjects were instructed to perform this movement over a nominal distance of 40 degrees in a self-paced manner. The total of 50 trials was performed.

Voluntary sway forward (VS)—This task was selected based on results from a previous study (Wang et al. 2006). In that study, data combined over different time samples within a sway cycle and across a few cycles were sufficient to identify muscle modes (see later). The subject stood upright on the force platform with his/her arms crossed on the chest. The subject was instructed to shift the body weight towards his/her toes and heels over the largest possible amplitude to determine the maximal COP_{AP} displacement avoiding toes off or heel off. Then, two horizontal target lines were added on the screen corresponding to 80% of the maximal COP_{AP} displacement both forward and backward with respect to the middle position. The

subjects were asked to occupy a body position corresponding to the backward target line and then sway to the forward line quickly and smoothly. If the trial showed hesitations, reversals, or undershoots or overshoots of over 20% of the total distance, the trial was discarded and repeated. The total of 15 successful trials was collected for each subject.

In each trial, data were collected over 6 s. The subjects heard a computer generated beep after data collection had begun, which indicated to them that they could initiate the required action. Subjects were reminded not to initiate their actions immediately after the beep, but to wait for about three seconds. The rest periods of at least 7 s between trials to re-establishing balance on the board and the rest periods of at least 5 min between conditions were given. Additional rest periods of about 1 min were given between sets of trials within the LR task and about 5 min after a half of the total number of trials within the AM task. Subjects reported no fatigue over the duration of the experiment. A period of familiarization with each condition was given to each subject prior to the very first session. On average, each subject was given two practice trials prior to each of the LR and AM tasks, and one minute of practice prior to the VS task.

Procedures

In a pilot study, all subjects could perform the LR and AM tasks without failures while standing on Board-1. In contrast, most subjects lost balance frequently when they performed these tasks while standing on a board with a 30 mm wide and 60 mm high beam. A failure (loss of balance) was determined when the edge of the board hit the platform within 5 s from the movement initiation. Therefore, during training we used boards fitted with two narrow beams (Board-A: 36 mm wide, 60 mm high; Board-B: 36 mm wide, 80 mm high) for practice, while the broader beam (50 mm wide and 60 mm high) was used during the testing sessions. Each subject started practicing on Board-A. When the number of failures at the task dropped under 10% of the total, Board-A was replaced with Board-B on the next day. The performance of the LR and AM tasks (performed on Board-1) was measured during three test sessions, prior to practice (pre-practice: PRE), following three days of practice (mid-practice: MID), and following five days of practice (post-practice: POST). The test sessions of MID and POST started after at least four hours after the end of practice on the same day. The performance of the VS task was measured during the PRE session under the stable condition only. The total number of trials during the practice and three test sessions under the unstable condition were 904 per subject.

In addition, four control trials were performed during the PRE-, MID-, and POST-test sessions. In the first and second control trials, the subjects were asked to stand as quietly as possible for 10 s under both stable and unstable conditions (Board-1). In the third and fourth control trials, the subjects were instructed to stand upright and hold a 4.0 Kg load in front of the body and behind the body through the pulley system for 10 s by pressing with the hands of the extended arms on a light horizontal handle under the stable condition. The pulley system redirected the load action upwards. These data were used for EMG normalization as described in the next subsection.

Data processing

All signals were processed off-line using LabView-8 and MatLab 7.3 software packages. The signal from the accelerometer was used for trial alignment. Individual LR and AM trials were viewed on a monitor screen and aligned according to the first change in the signal from the accelerometer (time zero: t_0) that could be identified by visual inspection at optimal resolution (Krishnamoorthy et al. 2003a, b). Signals from the force platform were filtered with a 20 Hz low-pass, second order, zero-lag Butterworth filter. For the voluntary sway trials, the initiation of sway (t_0) was defined as the time when the COP_{AP} derivative first exceeded 5% of its peak value in each single forward sway (Wang et al. 2006). COP_{AP} coordinate was computed using the following approximation:

$$\text{COP}_{\text{AP}} = \{F_y \times (a+h) + \Delta F_z \times b\} / F_z, \quad (1)$$

where coefficient a shows the distance of the platform surface from the sensor axis (0.022 m), coefficient b shows the distance of the sensor axis from x-axis (0.275 m) (Fig.1). Coefficient h shows the distance of the board surface from the platform surface under unstable condition (0.08 m), therefore h equals zero under the stable condition; coefficient a corresponds to the vertical distance from the platform surface to the center of the platform.

All EMG signals were rectified and filtered with a 50 Hz low-pass, second order, zero-lag Butterworth filter. Changes in the muscle activity associated with the early phase of the COP_{AP} shift were quantified as follows. For the LR trials, rectified EMG signals were integrated from 100 ms prior to t_0 up to t_0 ($\int \text{EMG}$). These values were corrected by EMG integrals quantified over a 100 ms time interval 400 ms prior to t_0 (see Eq. 2a):

$$\Delta/\text{EMG} = \int_{t_0-100}^{t_0} \text{EMG} dt - \int_{t_0-500}^{t_0-400} \text{EMG} dt \quad (2a)$$

For the AM trials, rectified EMG signals were integrated over 15 ms time intervals starting 300 ms prior to t_0 and ending up at (t_0+150) ms. Hence, the total of 30 time intervals were used. The 15 ms time intervals were selected as a compromise between having sufficient time resolution and avoiding to deal with point to point changes in the highly variable EMG signals. Note that our pilot studies have suggested that the results of analysis are robust with respect to the time bin size (unpublished). These EMG integrals were corrected by subtracting the EMG integrals during the control trial of quiet neutral stance under unstable condition. For this purpose, we selected the most stable 3 s period in the middle of the control trial by inspecting EMG signals from all the muscles. Further the integral over that time was divided by 200 to correspond to a 15 ms time window.

$$\Delta/\text{EMG}_j = \int_{t_0+15i}^{t_0+15*(i+1)} \text{EMG} dt - \frac{1}{200} \int_0^{3000} \text{EMG} dt, \quad (2b)$$

where $i = -20, -19, \dots, 0, 1, \dots, 10$ corresponding to different 15-ms intervals of data analysis.

For the VS trials, rectified EMG signals were integrated over 15 ms time intervals starting at t_0 and ending up at (t_0+300) ms. On average, the duration of a single forward sway half-cycle was about 450 ms. We chose the time window of 300 ms to avoid involving episodes associated with a change in the direction of COP_{AP} shift. These EMG integrals were corrected by subtracting the EMG integrals over a 15 ms time interval during the control trial of quiet neutral stance under stable condition. The equation was the same as Eq. 2b except with $i = 1, 2, \dots, 20$ corresponding to different 15-ms intervals of data analysis (Wang et al. 2006).

In order to compare Δ/EMG indices across muscles and subjects, we normalized them by the EMG integrals computed over the control trials when the subjects stood and held the 4.0 kg load. Δ/EMG indices for the dorsal (GL, GM, SOL, BF, ST and ES) muscles were divided by the EMG integrals ($\int \text{EMG}_C$) in the control trial with holding the load quietly in front of the body, while Δ/EMG indices for the ventral (TA, RF, VL, and RA) muscles, were divided by the EMG integrals ($\int \text{EMG}_C$) in the control trial with holding the load quietly behind the body (Krishnamoorthy et al. 2003a, b; Wang et al. 2005). The time intervals of $\int \text{EMG}_C$ were 100 ms for the LR trials and 15 ms for the AM and VS trials to match the integration intervals in Eqs (2a) and (2b).

$$\Delta/\text{EMG}_N = \Delta/\text{EMG} / \int \text{EMG}_C \quad (3)$$

For the LR trials, COP_{AP} shift corresponding to the EMG integral indices defined above was computed as the difference between the COP_{AP} position at time t_0+50 ms (50 ms following the interval of EMG integration) and the average COP_{AP} position measured between -200 ms

and -150 ms with respect to t_0 (a 50 ms time interval prior to the period of EMG integration). This comparison assumes an average 50 ms electromechanical delay (Corcos et al. 1992). For the LR and AM trials, COP_{AP} trajectory was computed with respect to time from 300 ms prior to t_0 up to (t_0+150 ms).

Statistics

Defining M-modes using principal component analysis (PCA)—For the VS task, for each subject, we got $\Delta IEMG_N$ data matrices with the size 80×10 (80 rows corresponding to the rectified EMG signals in each 15 ms time interval and 10 columns corresponding to the muscles). $\Delta IEMG_N$ data matrices were combined over four individual sways in the forward direction. For this analysis, we chose four individual sways with the half-cycle duration closest to 450 ms from the 15 trials at the VS task. For the LR task, for each subject, we got $\Delta IEMG_N$ data matrices with the size 63×10 (63 rows corresponding to the trials and 10 columns corresponding to the muscles). The correlation matrix among the $\Delta IEMG_N$ was subjected to PCA, using procedures from SPSS 14.0 (SPSS, Inc., Chicago, Illinois, USA). The factor analysis module with principal component extraction was employed.

For each subject, the obtained eigenvalues and PCs were then considered. The first three PCs for the VS and LR tasks were selected for further analysis. This was based on two criteria, examination of the scree plots (the following PCs accounted for approximately similar amounts of variance per PC) and having at least one muscle significantly loaded per PC (Krishnamoorthy et al. 2003a, Wang et al. 2005). We are going to address these PCs as muscle modes (M-modes) and assume that magnitudes of (coefficients at) the M-modes are manipulated by the controller to produce COP_{AP} shifts. In other words, M-modes represent unitary vectors in the muscle activation space that can be recruited by the controller with different magnitudes.

Defining the Jacobian using multiple regression—Linear relations between changes in the magnitudes of M-modes (M) and the COP_{AP} shifts (COP_{AP}) were assumed and the corresponding multiple regression equations computed over the trials performed by each subject separately. The coefficients of each regression equation were arranged in a matrix that is a Jacobian matrix. The VS and LR tasks were used to generate linear estimates of the following Jacobian (J_{AP}):

$$\Delta COP_{AP} = k_1 \Delta M_1 + k_2 \Delta M_2 + k_3 \Delta M_3 \quad ; \quad J_{AP} = [k_1 k_2 k_3]^T \quad (4)$$

within this approach, the J matrices are reduced to (3×1) vector-columns. For the VS task, for each subject, this analysis was run over ΔM data matrices with the size 80×3 , which were combined over the four selected individual sways in the forward direction, and the corresponding ΔCOP_{AP} within each 15-ms time interval. For the LR task, for each subject, this analysis was run over ΔM data matrices with the size 63×3 , which were combined over all the trials, and the corresponding ΔCOP_{AP} as the difference between the COP_{AP} position at time t_0+50 ms and the average COP_{AP} position measured between -200 ms and -150 ms with respect to t_0 .

UCM analysis: Index of synergy—For each trial of the AM task, $\Delta IEMG_N$ were computed and transformed into ΔM using the results of the PCA. The ΔM space has dimensionality $n=3$. A hypothesis that a particular magnitude of ΔCOP_{AP} is stabilized by co-variation of ΔM magnitudes accounts for one degree of freedom ($d = 1$). Thus, the system is redundant with respect to the task of stabilizing particular ΔCOP_{AP} values. The mean magnitudes for each ΔM were computed across a series of trials. Since the model relating ΔM to ΔCOP_{AP} is linear, the ΔM mean values were subtracted from each ΔM computed value and the residuals were further analyzed as follows.

The UCM represents combinations of M-modes that are consistent with a stable value of $\Delta\text{COP}_{\text{AP}}$. Therefore, the UCM was calculated as the null space of the corresponding $\mathbf{J}$ matrix. The null space of $\mathbf{J}$ is a set of all vector solutions $\mathbf{x}$ of a system of equations $\mathbf{J}\mathbf{x}=\mathbf{0}$. The null space is spanned by basis vectors, $\mathbf{e}_i$. The vector of individual mean-free ΔMs was resolved into its projection onto the null space:

$$f_{\text{UCM}} = \sum_{i=1}^{n-d} \left(\mathbf{e}_i^T \cdot (\Delta\mathbf{M}) \right) \mathbf{e}_{-i} \quad (5a)$$

and component orthogonal to the null space:

$$f_{\text{ORT}} = (\Delta\mathbf{M}) - f_{\text{UCM}} \quad (5b)$$

The amount of variance per DOF within the UCM is:

$$V_{\text{UCM}} = \sigma_{\text{UCM}}^2 = \sum_{i=1}^N f_{\text{UCM}}^2 / ((n-d) N_{\text{trials}}) \quad (6a)$$

and orthogonal to the UCM is:

$$V_{\text{ORT}} = \sigma_{\text{ORT}}^2 = \sum_{i=1}^N f_{\text{ORT}}^2 / (d N_{\text{trials}}) \quad (6b)$$

V_{UCM} and V_{ORT} were the main dependent variables used in the study. To quantify the relative amount of the total variance that is compatible with stabilization of a particular shift of the COP_{AP} we used a variable (ΔV) reflecting the normalized difference between V_{UCM} and V_{ORT} . It was computed as:

$$\Delta V = (V_{\text{UCM}} - V_{\text{ORT}}) / V_{\text{TOT}} \quad (7)$$

where all variance indices are computed per degree of freedom; V_{TOT} means the total variance.

We used Friedman's test on the number of error trials under the two practice conditions (LR and AM) across subjects, and on the number of occurrences of the three types of M-modes (for details see Results) under the stable condition for the VS task and under the unstable condition for the LR task across subjects. Further pair-wise comparison was performed using Wilcoxon's test. Two-way mixed-design ANOVA was used with factors *Test-Session* (PRE, MID and POST) and *Variance* (V_{UCM} and V_{ORT}) to analyze possible differences in the values of these two variance indices across the test sessions. The analyses were performed separately for three 150 ms time intervals starting 300 ms prior to t_0 and ending up to (t_0+150 ms). The selection of these time windows was based on earlier studies that showed anticipatory changes in ΔV about 150 ms prior to action initiation (Olafsdottir et al. 2005; Shim et al. 2005). In addition, two-way mixed-design ANOVA was used with factors *Test-Session* (PRE, MID and POST) and *Time-Interval* (from -300 to -150 ms prior to t_0 , from -150 ms prior to t_0 to t_0 and from t_0 to +150 ms after t_0) to analyze ΔV changes across the sessions and at different phases of the AM task. Further pair-wise comparison was performed using Student's *t*-test with Bonferroni corrections. Statistical significance was set at $p < 0.05$.

Results

Incidence of balance loss

During the load release (LR) and arm movement (AM) tasks performed while standing on an unstable board, in most subjects, the number of trials when the subjects lost balance decreased rapidly for both tasks. Seven out of the eight subjects improved their performance to a degree that allowed them to switch from a less challenging condition (Board-A) to a more challenging

board (Board-B) by the fourth day of practice. Figure 2 shows the percentage of trials with lost balance (error trials) out of the total of 63 trials for the LR task and out of the total of 50 trials for the AM task under the unstable condition for each subject. The filled circles and open circles show the percentage of error trials under the Board-A and Board-B condition, respectively. Friedman's test showed that the number of error trials for the six subjects who had practiced on Board-A over the first three days of practice sessions decreased significantly for both tasks (LR: $n = 6$, $df = 2$, $p < 0.01$; AM: $n = 4$, $df = 2$, $p < 0.05$). For the AM task, the number of error trials for the seven subjects who had practiced on the Board-B decreased significantly over the last two days of practice ($n = 7$, $df = 1$, $p < 0.01$).

General COP_{AP} and EMG patterns

Figure 3 shows COP_{AP} shift and normalized EMG time profiles from eight of the ten postural muscles under the unstable condition in a representative subject performing the LR and AM tasks across the three test sessions. Note that in the test sessions, Board-1 was always used with the beam 5 cm wide and 6 cm high. Figure 3A shows the average value across the nine trials during the LR task performed using the 4.0 Kg load, while Figure 3B shows the average value across the 50 trials during the AM task. The data before practice, in the middle of practice, and at the end of practice (PRE, MID and POST sessions) are shown with thin solid lines, thick dotted lines and thick solid lines, respectively. The COP_{AP} shifts and EMG patterns were qualitatively similar across the three sessions for each task. In general, there was an increase in the dorsal muscle (GM, SOL, BF, ST and ES) activity prior to the initiation of action (t_0). There could also be a decrease in some of the ventral muscle (TA, RF and RA) activity. Muscle activity varied across subjects, and some subjects did not show clear bursts or suppression of EMG in some muscles.

PCA of the data obtained in the VS and LR tasks

Indices of integrated muscle activity were measured over short time intervals during the VS task under the stable condition and during the LR task under the unstable condition for all muscles (Δ IEMG indices, see the Methods). These indices were normalized by the integrated muscle activity during control trials resulting in Δ IEMG_N. The Δ IEMG_N indices for each subject were subjected to PCA. Consistent with previous studies (Krishnamoorthy et al., 2003a, Wang et al. 2005), across all subjects for three test sessions, we found that the first three PCs (PC₁, PC₂ and PC₃) had at least one muscle index significantly loaded. Principal components from PC₄ onward explained little variance in the Δ IEMG_N space and were poorly reproducible across subjects.

For the data from the VS trials, the first three PCs accounted, on average, for 61.7% ($\pm 2.5\%$ SE; ranging from 53.1% to 74.4%) of the total variance. For the data from the LR trials, the first three PCs accounted on average for 64.0% $\pm 3.5\%$ (ranging from 52.5% to 77.0%) of the total variance during the PRE session, 64.4% $\pm 3.0\%$ (ranging from 52.8% to 75.7%) of the total variance during the MID session, and 62.6% $\pm 2.2\%$ (ranging from 54.4% to 72.5%) of the total variance during the POST session (means and standard errors are shown; see Table 1). Z-scores for the fractions of variance explained were computed to assess differences across the tests. One-way ANOVA with the factor *Test session* (PRE, MID and POST) run for variance explained by each PC separately showed no significant differences across the three test sessions.

Across all subjects and conditions, we found three types of PCs (M-modes) based on muscles that loaded significantly (with the absolute value of the loading factor over 0.5; Hair et al. 1995). These are illustrated in Figure 4. We will address the two basic types as "reciprocal" and "co-contraction" (Krishnamoorthy et al. 2004; panel A in Figure 4). There were two types of reciprocal M-modes, "push-back" (M₁-mode) and "push-forward" (M₂-mode). There were

three types of co-contraction M-modes, “co-contraction at the hip” (M₃-mode), “co-contraction at the knee” (M₄-mode), and “co-contraction at the ankle” (M₅-mode). We classified the combination of the medial head of gastrocnemius (GM) and vastus lateralis (VL) as a co-contraction M-mode at the knee (M₄) since the medial head of gastrocnemius is a biarticular muscle with a flexion action at the knee joint. The muscles indicated in *italics* in Figure 4 did not show up consistently in the modes indicated.

M-modes of the third type, “mixed M-modes”, could involve co-activation at one of the joints in addition to at least two more muscles loaded significantly on the same side of the body, dorsal or ventral. Figure 4B shows typical combinations of muscles involved in mixed M-modes. We found five types of the mixed M-modes, which could be viewed as combinations of “reciprocal” and “co-contraction” M-modes. These types were the combination of “co-contraction at the hip” and “push-back” (Mix 1) or “push-forward” (Mix 2), “co-contraction at the ankle” and “push-back” (Mix 3) or “push-forward” (Mix 4) and “co-contraction at the knee” and “push-back” (Mix 5). In rare cases, when only one muscle loaded significantly on one of the first three PCs, this mode was not classified as any of those mentioned, but addressed as a “Singular” mode.

Changes in the M-modes with practice

In the PRE session, six subjects showed only reciprocal M-modes under the stable condition. In contrast, all eight subjects showed co-contraction modes and/or mixed modes under the unstable condition. For quantitative analysis, we first classified the M-modes according to the definition illustrated in Figure 4, and then calculated the number of times the reciprocal M-modes occurred. Further, we summed up the number of times co-contraction and mixed M-modes were seen in each condition and test session for each subject (see Table 2). Wilcoxon’s test showed that the number of times the co-contraction and mixed M-modes were seen under the unstable condition was significantly larger than that under the stable condition ($p < 0.05$), while the number of times the reciprocal M-modes occurred under the unstable condition was significantly smaller than that under the stable condition ($p < 0.05$) (Fig.5).

Similar analysis was performed after practice. Friedman’s test on the number of times M-modes occurred, across the PRE, MID and POST sessions has shown a significant difference among the three test sessions in the occurrence of both the reciprocal M-modes and the combined co-contraction and mixed M-modes ($n=8$, $df=2$, $p < 0.05$). Wilcoxon’s test showed that the occurrence of co-contraction and mixed M-modes in the middle of practice was significantly smaller than that before practice ($p < 0.05$). In contrast, the occurrence of reciprocal M-modes after practice was significantly larger than that in the middle of the practice ($p < 0.05$) (Fig.5).

Identifying the Jacobians: results of multiple regression analyses

The linear relations between changes in the magnitudes of M-modes (ΔM s) and the associated COP_{AP} shifts ($\Delta \text{COP}_{\text{AP}}$) were assumed and computed using multiple regression analysis. This was done using data for the VS and LR tasks in the three test sessions separately. As a result, one set of regression coefficients (Jacobian) was computed for each of the three test sessions. The three M-modes could be associated with either basic or mixed M-modes, and could change with practice. However, variations in the magnitudes (gains at) three M-modes explained similar amounts of variance (estimated through the coefficient of determination) in $\Delta \text{COP}_{\text{AP}}$ across the four conditions. Under the stable condition, variation in the magnitudes of the three M-modes accounted for 68% ($\pm 2\%$ SE) of the total variance in $\Delta \text{COP}_{\text{AP}}$. For the PRE, MID and POST sessions, variation in the magnitudes of the three M-modes accounted for 72% ($\pm 2\%$ SE), 72% ($\pm 4\%$ SE) and 68% ($\pm 4\%$ SE) of the total variance in $\Delta \text{COP}_{\text{AP}}$, respectively. One-way repeated measures ANOVA with the factor *Condition* (STABLE, PRE, MID and POST) showed no significant effect of *Condition* [$F_{(3,18)} = 0.48$, $p > 0.7$].

UCM analysis of the AM task

Data from the quick arm extension movement (AM) task were used to perform analysis of the structure of variability across 50 trials in the space of magnitudes of M-modes. The method partitioned the total variance in the M-mode space across trials into two components. The first component (V_{UCM}) was within an uncontrolled manifold (UCM) computed as the null-space of a corresponding $\mathbf{J}$ matrix defined at the previous step of analysis. The other component (V_{ORT}) was within a sub-space orthogonal to the UCM. Both V_{UCM} and V_{ORT} were quantified per degree-of-freedom in corresponding subspaces. Further, to quantify the relative amount of the total variance that is compatible with a certain value of the COP_{AP} shift (estimated as the average across trial value) we used an index ΔV reflecting the difference between V_{UCM} and V_{ORT} . Positive values of ΔV showed that more variance per degree-of-freedom was within the UCM than within its orthogonal complement; we interpret this result as the existence of a multi-M-mode synergy that stabilizes the COP_{AP} shift. Negative ΔV values imply destabilization of the average COP_{AP} shift by co-varied changes in magnitudes of the M-modes.

Figure 6 illustrates typical changes of ΔV associated with the quick arm movement under the unstable condition for a representative subject. Time zero (t_0) was defined by the signal from the accelerometer taped on the subject's right hand. The data for the PRE, MID and POST sessions are shown with thin solid line, thick dotted line and thick solid line, respectively. Prior to the practice sessions, the subject showed consistently negative values of ΔV both prior to and after the arm movement. Positive ΔV values were seen in the MID and POST sessions. In the MID session, an abrupt drop in ΔV was observed close to the time of action initiation (t_0). This drop disappeared at the POST session.

To perform across-subjects analysis of the M-mode synergies related to stabilization of the COP_{AP} position, the two variance components and ΔV indices were averaged over three 150 ms time intervals (T1: from -300 to -150 ms prior to t_0 , T2: from -150 ms prior to t_0 to t_0 and T3: from t_0 to +150 ms after t_0). To analyze the effects of practice on the two variance components, a two-way ANOVA with repeated measures, with the factors *Test-session* (PRE, MID and POST) and *Variance* (V_{UCM} and V_{ORT}) was performed for each time interval (T1, T2 and T3) (Fig. 7). For the second time interval T2 (between -150 ms prior to t_0 and t_0), there was a significant main effect of *Test-session* [$F_{(2,14)} = 7.06$, $p < 0.01$] without a significant interaction. Bonferroni pair-wise contrasts showed that the two variance components during the MID session were significantly smaller than those at the PRE session. For the third time interval T3 (between t_0 and +150 ms after t_0), there was a significant interaction [$F_{(2,14)} = 16.82$, $p < 0.01$] without significant main effects. Bonferroni pair-wise contrasts showed that V_{ORT} was significantly larger than V_{UCM} during the PRE session. In contrast, V_{ORT} was significantly smaller than V_{UCM} during the POST session. There were no significant effects and no interaction for the first time interval T1 (between -300 and -150 ms prior to t_0).

Figure 8 shows ΔV indices across subjects over the three time intervals for each test session. A two-way ANOVA with repeated measures, with the factors *Test-session* (PRE, MID and POST) and *Time-interval* (T1, T2 and T3) showed that there was a significant main effect of *Test-session* [$F_{(2,14)} = 6.52$, $p < 0.01$] without a significant interaction. Bonferroni pair-wise comparisons showed that ΔV at POST session was significantly larger than that at PRE session.

Discussion

All three questions formulated in the Introduction received affirmative answers in the experiments. A change in the postural stability conditions led to a significant increase in the incidence of co-contraction and mixed M-modes (cf. Krishnamoorthy et al. 2004). The number of such M-modes dropped significantly with practice. This was associated with the emergence and strengthening of multi-M-mode synergies stabilizing shifts of the center of pressure. Taken

together, these findings have important implications for a variety of issues related to postural control and the organization of multi-muscle synergies.

Modes as elemental variables

We would like to emphasize a major difference of our approach from those of a number of research groups who have also used matrix factorization techniques to identify muscle groups, within which levels of muscle activation scaled in parallel (d'Avella et al. 2003; Ivanenko et al. 2004; Weiss and Flanders 2004; Ting and Macpherson 2005; Tresch et al. 2006). Both lines of research follow the general idea that a smaller number of variables (M-modes in our study or “synergies” in most other studies) can be used to construct behaviors with different characteristics (Loeb et al. 2000; Saltiel et al. 2001; d'Avella and Bizzi 2005; Ting and Macpherson 2005). A recent comparison of different methods to identify such M-modes (“synergies”) has suggested that the results are robust across a variety of methods including principal component analysis and independent component analysis (Tresch et al. 2006).

Most other groups suggest that various behaviors are created by combining a number of “synergies” (modes) with different gains. This may be associated with one of the major characteristics of synergies, namely sharing (Li et al. 1998; Gelfand and Latash 1998, 2002). Our analysis goes a step further to quantify another major feature of synergies that has been addressed as stability/flexibility (reviewed in Latash et al. 2007). We searched for synergies in the space of M-modes rather than in the space of original muscle activations because within the muscle activation space one could expect task-independent co-variation among muscle activation indices that could potentially lead to a spurious false conclusion on a synergy being present or absent (for more detail see Krishnamoorthy et al. 2003a,b).

The difference between the two approaches may be illustrated using a simple example of producing a required value of the total force (F_{TOT}) by pressing with two fingers on two force sensors. Finger forces are non-independent due to the phenomenon of enslaving (Li et al. 1998; Zatsiorsky et al. 2000). Hence, analysis of such tasks has been performed using another set of hypothetical variables, finger modes (Latash et al. 2001; Scholz et al. 2002), analogous to M-modes in the current study. In the finger mode space, the required value of F_{TOT} may be produced with different combinations of modes (Figure 9). Three clouds of data points in such a mental experiment are illustrated in Figure 9. The spherical distribution of data points (D_1) corresponds to a non-synergy in our terms. The ellipse elongated along the solid slanted line whose points correspond to the required value of F_{TOT} shows mode co-variation that is beneficial for F_{TOT} stabilization - a force stabilizing synergy (D_2). The ellipse elongated orthogonal to that line corresponds to mode co-variation that destabilizes F_{TOT} (D_3). The average location (solid dots) of the clouds of data points shown in Figure 9 corresponds to the sharing feature of the two-finger synergy, while the shape of the data point clouds reflects the stability/flexibility feature. We did not analyze the average sharing among the M-modes within this study (reflected in the regression coefficients forming the Jacobian) because we designed it to focus on possible changes in the composition of M-modes and co-variation among the M-modes.

Stability and flexibility of modes

The idea of structural units (synergies, in the current study) originally proposed by Gelfand and Tsetlin (1966) has assumed that any element of a structural unit is itself a structural unit at a different level of analysis. Hence, synergies are based on co-variation of elemental variables that are assumed to be relatively stable (showing little change) at typical time scales associated with motor actions that the synergies stabilize. For example, previous studies have shown changes in the index of multi-M-mode synergies during the execution of such tasks as making a step and voluntary sway (Wang et al. 2005, 2006). These studies assumed that no changes

in the composition of M-modes happened during the execution of such tasks. This assumption has been indirectly corroborated by the observations of similar M-modes in several studies using variations of postural tasks (Krishnamoorthy et al. 2003b; Wang et al. 2005, 2006; Danna-Dos-Santos et al. 2007).

At a different time scale, however, elemental variables (M-modes) may themselves show changes. Our study demonstrates that this is indeed so. First, M-modes reorganized when the subjects performed postural tasks under challenging conditions (while standing on a board with a narrow support surface) corroborating earlier observations (Krishnamoorthy et al. 2004). Besides, practice of such tasks resulted in a gradual change in the M-mode composition with a drop in the occurrence of co-contraction modes. Hence, M-modes are stable within a broad range of postural tasks but they can change with significant changes in postural stability conditions as well as with practice.

The observation of co-contraction M-modes fits well several studies that have reported predominance of muscle co-contraction patterns in postural tasks performed under challenging conditions (Shiratori and Latash 2000) as well in persons with an impaired postural control due to aging (Hatzitaki et al. 2005) or a neurological disorder (Ioffe et al. 2006). We view as encouraging our observations of changes in the M-mode composition with practice. These observations allow us to hope that practice can lead to improved postural synergies in persons with impaired balance.

Effects of practice on modes and synergies

To our knowledge, the current study is the first to address effects of practice on muscle synergies at two levels of a hypothetical hierarchy. Within this hierarchy, the upper level manipulates coefficients of involvement of elemental variables that serve as inputs into the lower level. At the lower level, the elemental variables project on muscles resulting in parallel scaling of muscle activation (observed as M-modes).

Effects of practice on motor synergies have been studied using the framework of the UCM hypothesis. These studies have shown that indices of synergies can increase with practice (Kang et al. 2004; Latash et al. 2003), or decrease (Domkin et al. 2002), or stay unchanged (Domkin et al. 2005). A conclusion has been drawn that early stages of practice of a novel task are characterized by emergence and strengthening of synergies stabilizing important performance variables. At later stages, more stereotypical solutions may develop leading to a drop in the synergy index. This may be caused by the controller trying to optimize features of performance that are beyond the explicit task (for example, related to such factors as comfort, energy expenditure, fatigue, etc.). In the current study, we observed results compatible with the first stage; it is possible that further practice would lead to a drop in the index of COP stabilizing synergies. Our subjects showed an increase in the synergy index with practice, which happened in parallel with changes in the composition of M-modes. This is a non-trivial result since changes in the composition of elemental variables may be expected to lead to problems for the controller that tries to use these changing variables to form synergies.

Earlier studies of the effects of fatigue on finger interaction (Danion et al. 2000, 2001) have shown that fatigue can lead to changes in the enslaving (unintended force production, Li et al. 1998) across the fingers of the hand. Since patterns of enslaving have been used to reconstruct finger modes - hypothetical elemental variables forming the basis for multi-finger synergies (Latash et al. 2001; Danion et al. 2003) - this finding implies changes in the elemental variables under fatigue. To our knowledge, the studies of Danion and his colleagues have been the only ones that addressed, albeit indirectly, the issue of possible changes in elemental variables. Our current study shows directly that the composition of muscle modes can change with practice. This finding shows that effects of practice on motor coordination may involve changes at

different levels of the hierarchical control system and that interactions among different hierarchical levels have to be considered in studies of the effects of practice and rehabilitation on motor coordination.

Implications for the field of motor learning

Traditionally, studies of motor learning focus on certain performance variables such as force, speed, and movement time, that are directly related to the task (Schmidt 2004). Practice is expected to lead to a change in the average magnitude of such variables (commonly, maximize or minimize them) and a drop in their variability. Effects of motor learning on coordination within multi-element systems has been discussed within the classical Bernstein scheme of stages such as freezing and releasing degrees-of-freedom (Bernstein 1996; Vereijken et al. 1992; Newell et al. 2003).

Our approach is substantially different. Based on the principle of abundance (Geldman and Latash 1998), we do not expect the number of degrees-of-freedom (elemental variables) to change with practice. Rather we expect the controller to optimize its handling of all the available degrees-of-freedom. In particular, changes in the composition of elemental variables and patterns of their co-variation with respect to important performance variables may be expected. Both can potentially lead to an improvement in patterns and indices of those performance variables such as their rate of change and variability. The current results provide support for this general attitude to motor learning by showing changes in both elemental variables and synergies based on these variables .

Acknowledgements

This work was supported in part by the Japanese Ministry of Education and Science (18500394) and by a National Institutes of Health (USA) grant NS-035032.

References

- Aruin AS, Latash ML. Anticipatory postural adjustments during self-initiated perturbations of different magnitude triggered by a standard motor action. *Electroencephalogr Clin Neurophysiol* 1996;101:497–503. [PubMed: 9020822]
- Belen’kii VY, Gurfinkel VS, Paltsev YI. Elements of control of voluntary movements. *Biofizika* 1967;12:135–141. [PubMed: 5623488]
- Bernstein, NA. The coordination and regulation of movements. Pergamon Press; London: 1967.
- Bernstein, NA. On dexterity and its development. In: Latash, ML.; Turvey, MT., editors. *Dexterity and Its Development*. Erlbaum Publ.; Mahwah, NJ: 1996. p. 3-246.
- Danion F, Latash ML, Li ZM, Zatsiorsky VM. The effect of fatigue on multifinger co-ordination in force production tasks in humans. *J Physiol* 2000;523:523–32. [PubMed: 10699094]
- Danion F, Latash ML, Li ZM, Zatsiorsky VM. The effect of a fatiguing exercise by the index finger on single- and multi-finger force production tasks. *Exp Brain Res* 2001;138:322–329. [PubMed: 11460770]
- Danion F, Schöner G, Latash ML, Li S, Scholz JP, Zatsiorsky VM. A mode hypothesis for finger interaction during multi-finger force-production tasks. *Biol Cybern* 2003;88:91–98. [PubMed: 12567224]
- 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]
- D’Avella A, Bizzi E. Shared and specific muscle synergies in natural motor behaviors. *Proc Natl Acad Sci USA* 2005;102:3076–3081. [PubMed: 15708969]

- Domkin D, Laczko J, Jaric S, Johansson H, Latash ML. Structure of joint variability in bimanual point tasks. *Exp Brain Res* 2002;143:11–23. [PubMed: 11907686]
- Domkin D, Laczko J, Djupsjobacka M, Jaric S, Latash ML. Joint angle variability in 3D bimanual pointing: uncontrolled manifold analysis. *Exp Brain Res* 2005;163:44–57. [PubMed: 15668794]
- Gelfand IM, Latash ML. On the problem of adequate language in motor control. *Motor Control* 1998;2:306–313. [PubMed: 9758883]
- Gelfand, IM.; Latash, ML. On the problem of adequate language in biology. In: Latash, ML., editor. *Progress in Motor Control. vol. 2: Structure-Function Relations in Voluntary Movement*. Human Kinetics; Urbana, IL: 2002. p. 209-228.
- Gelfand, IM.; Tsetlin, ML. On mathematical modeling of the mechanisms of the center nervous system. In: Gelfand, IM.; Gurfinkel, VS.; Fogt, N.; Tsetlin, ML., editors. *Models of the structural-functional organization of certain biological systems*. Nauka; Moscow: 1966. p. 9-26.
- Hatzitaki V, Amiridis IG, Arabatzis F. Aging effects on postural responses to self-imposed balance perturbations. *Gait Posture* 2005;22:250–257. [PubMed: 16214664]
- Ioffe ME, Ustinova KI, Chernikova LA, Kulikov MA. Supervised learning of postural tasks in patients with poststroke hemiparesis, Parkinson's disease or cerebellar ataxia. *Exp Brain Res* 2006;168:384–394. [PubMed: 16175360]
- 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]
- Ivanenko YP, Cappellini G, Dominici N, Poppele RE, Lacquaniti F. Coordination of locomotion with voluntary movements in humans. *J Neurosci* 2005;25:7238–7253. [PubMed: 16079406]
- Kang N, Shinohara M, Zatsiorsky VM, Latash ML. Learning multi-finger synergies: an uncontrolled manifold analysis. *Exp Brain Res* 2004;157:336–350. [PubMed: 15042264]
- Krishnamoorthy V, Goodman S, Zatsiorsky VM, Latash ML. 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: effect of instability and additional support. *Exp Brain Res* 2004;157:18–31. [PubMed: 14985897]
- Latash ML, Scholz JP, Danion F, Schöner G. Structure of motor variability in marginally redundant multifinger force production tasks. *Exp Brain Res* 2001;141:153–165. [PubMed: 11713627]
- Latash ML, Scholz JP, Schöner G. Motor control strategies revealed in the structure of motor variability. *Exer Sport Sci Rev* 2002;30:26–31.
- Latash ML, Yarrow K, Rothwell JC. Changes in finger coordination and responses to single pulse TMS of motor cortex during practice of a multifinger force production task 2003;151:60–71.
- Latash ML, Anson JG. Synergies in health and disease: relations to adaptive changes in motor coordination. *Phys Ther* 2006;86:1151–1160. [PubMed: 16879049]
- Latash ML, Scholz JP, Schöner G. Toward a new theory of motor synergies. *Motor Control* 2007;11:275–307.
- Li ZM, Latash ML, Zatsiorsky VM. Force sharing among fingers as a model of the redundancy problem. *Exp Brain Res* 1998;19:276–286. [PubMed: 9551828]
- Loeb EP, Giszter SF, Saltiel P, Bizzi E, Mussa-Ivaldi FA. Output units of motor behavior: an experimental and modeling study. *J Cogn Neurosci* 2000;12:78–97. [PubMed: 10769307]
- Newell KM, Broderick MP, Deutsch KM, Slifkin AB. Task goals and change in dynamical degrees of freedom with motor learning. *J Exp Psychol: Hum Percept Perform* 2003;29:379–87. [PubMed: 12760622]
- 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]
- Saltiel P, Wyler-Duda K, D'Avella A, Tresch MC, Bizzi E. Muscle synergies encoded within the spinal cord: evidence from focal intraspinal NMDA topophoresis in the frog. *J Neurophysiol* 2001;85:605–619. [PubMed: 11160497]

- Schmidt, RA. Motor learning and performance. Human Kinetics; Champaign, IL: 2004.
- Shim JK, Olafsdottir H, Zatsiorsky VM, Latash ML. The emergence and disappearance of multi-digit synergies during force-production tasks. *Exp Brain Res* 2005;164:260–270. [PubMed: 15770477]
- 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, Danion F, Latash ML, Schöner G. Understanding finger coordination through analysis of the structure of force variability. *Biol Cybern* 2002;86:29–39. [PubMed: 11918210]
- Shiratori T, Latash M. The roles of proximal and distal muscles in anticipatory postural adjustments under asymmetrical perturbations and during standing on rollerskates. *Clin Neurophysiol* 2000;111:613–623. [PubMed: 10727912]
- Shiratori T, Aruin A. Modulation of anticipatory postural adjustments associated with unloading perturbation: effect of characteristics of a motor action. *Exp Brain Res* 2007;178:206–215. [PubMed: 17109110]
- 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]
- Tresch MC, Cheung VC, D’Avela A. Matrix factorization algorithms for the identification of muscle synergies: evaluation of simulated and experimental data sets. *J Neurophysiol* 2006;95:2199–212. [PubMed: 16394079]
- Vereijken B, van Emmerick REA, Whiting HTA, Newell KM. Free(z)ing degrees of freedom in skill acquisition. *J Mot Behav* 1992;24:133–142.
- Wang Y, Zatsiorsky VM, Latash ML. Muscle synergies involved in shifting the center of pressure while making a first step. *Exp Brain Res* 2005;167:196–210. [PubMed: 16034579]
- Wang Y, Asaka T, Zatsiorsky VM, Latash ML. Muscle synergies during voluntary body sway: combining across-trials and within-a-trial analyses. *Exp Brain Res* 2006;174:679–693. [PubMed: 16710681]
- Weiss EJ, Flanders M. Muscular and postural synergies of the human hand. *J Neurophysiol* 2004;92:523–535. [PubMed: 14973321]
- Zatsiorsky VM, Li ZM, Latash ML. Enslaving effects in multi-finger force production. *Exp Brain Res* 2000;131:187–195. [PubMed: 10766271]

Figure 1.

The experimental setup: The subjects stood on the force platform (the “stable condition”) or on a specially constructed wooden board (the “unstable condition”). The board was fitted with a narrow beam on the undersurface. This board was placed over the force platform such that its narrow dimension was in the anterior-posterior (AP) direction. For the load release task, the subject held a load suspended behind the body through the pulley system and then released the load quickly. Location of some of the EMG electrodes is also shown (*TA* tibialis anterior, *GL* lateral head of gastrocnemius, *GM* medial head of gastrocnemius, *SOL* soleus, *RF* rectus femoris, *VL* vastus lateralis, *BF* biceps femoris, *ST* semitendinosus, *RA* rectus abdominis, and *ES* erector spinae); acc - accelerometer.

Figure 2.

Changes in performance errors with practice: The percentage of the number of error trials for the consecutive five practice days for the two tasks (A: load release task, B: arm movement task). The filled circles and open circles show the data for Board-A and Board-B, respectively. When the percentage of errors dropped under 10% (the horizontal dashed lines), Board-A was replaced with Board-B on the next day.

Figure 3.

Displacement of the center of pressure in the anterior-posterior direction (COP_{AP}) and normalized EMG patterns for a representative subject who performed the load release task with the load of 4 kg (A) and the arm movement task (B) in the three test sessions: Pre-practice (PRE: *thin line*), mid-practice (MID: *thick dashed line*) and post-practice (POST: *thick line*) while standing on Board-1. The time of the action initiation is shown as time zero (t_0) with vertical lines. Averages across nine trials (load release) and 50 trials (arm movement) are shown. COP_{AP} displacement in the anterior direction is shown as positive (Fig.3a, b). The scales have been selected for better visualization.

Figure 4.

The diagram of classification of muscle modes (M-modes) based on results of the PCA. There were two types of “reciprocal modes”, three types of “co-contraction modes”, and five types of “mixed modes”. The muscles indicated in *italics* did not show up consistently in the PC indicated. *TA* tibialis anterior, *GL* lateral head of gastrocnemius, *GM* medial head of gastrocnemius, *SOL* soleus, *RF* rectus femoris, *VL* vastus lateralis, *BF* biceps femoris, *ST* semitendinosus, *RA* rectus abdominis, and *ES* erector spinae.

Figure 5.

The total range (min - max), the 25-75% range, and the median for the number of times the reciprocal M-modes and the total of the co-contraction and mixed M-modes were seen across subjects. *STABLE* - stable condition, *PRE* - pre-practice under unstable condition, *MID* - mid-practice under unstable condition, *POST* - post-practice under unstable condition. Note that the co-contraction and mixed M-modes occurred more frequently at the PRE test as compared to the STABLE test. Then, their number dropped with practice. * $p < 0.05$

Figure 6.

Typical changes of the index of multi-mode synergy, ΔV during quick arm extension movements by a representative subject in the three test sessions, pre-practice (*thin line*), mid-practice (*thick dashed line*) and post-practice (*thick line*) while standing on Board-1 (unstable condition). The time of action initiation is shown as time zero (t_0 , the vertical dashed line). The data are shown for 15 ms time intervals. Before practice, the subject showed consistently negative values of ΔV ; these values turned positive during the other two sessions. No drop in ΔV after the action initiation can be seen in the post-practice session.

Figure 7.

The two variance components (V_{UCM} : black bars and V_{ORT} : open bars) averaged across subjects for the arm movement task in the three test sessions (*PRE*, *MID* and *POST*) with standard error bars. The data were averaged over three 150 ms time intervals (*T1*: from -300 to -150 ms prior to t_0 , *T2*: from -150 ms prior to t_0 to t_0 and *T3*: from t_0 to +150 ms after t_0). * $p < 0.05$

Figure 8.

The ΔV indices averaged across subjects for the arm movement task in the three test sessions (*PRE*, *MID* and *POST*) with standard error bars. The ΔV indices were averaged over three 150 ms time intervals. The open, striped and black bars correspond to the time interval from -300 to -150 ms prior to t_0 (*T1*), from -150 ms prior to t_0 to t_0 (*T2*) and from t_0 to +150 ms after t_0 (*T3*), respectively. Note that ΔV after practice was significantly larger than that before practice.

* $p < 0.05$.

Figure 9.

An illustration of the two features of synergies using an example of producing a value of the total force with two fingers. Clouds of data points are shown in the finger mode space. The solid slanted line corresponds to perfect task performance. The three clouds correspond to different sharing patterns reflected in different average locations (black dot). The spherical distribution of data points (D_1) shows no co-variation between the modes that would stabilize the total force. The ellipse elongated along the solid slanted line (D_2) shows mode co-variation that is beneficial for F_{TOT} stabilization - a force stabilizing synergy. The ellipse elongated orthogonal to that line (D_3) corresponds to mode co-variation that destabilizes F_{TOT} .

Table 1

Total variance explained by the first three principal components

Condition		PC ₁	PC ₂	PC ₃
stable	Mean	27.7	18.9	15.1
	SE	2.4	1.0	1.0
	Range	21.8-40.7	13.7-21.2	12.1-20.5
unstable	Mean	28.2	19.7	16.0
	SE	3.1	0.7	0.4
	Range	18.6-39.0	17.3-21.7	14.7-17.4
PRE	Mean	32.9	17.3	14.2
	SE	3.4	1.0	0.8
	Range	22.0-49.0	14.9-22.5	11.1-18.2
MID	Mean	27.2	19.7	15.6
	SE	2.9	0.7	0.9
	Range	21.0-40.5	17.8-24.2	11.9-18.7
POST	Mean	27.2	19.7	15.6
	SE	2.9	0.7	0.9
	Range	21.0-40.5	17.8-24.2	11.9-18.7

Mean values, standard errors, and ranges are shown for the percentage of the total variance accounted for by the first three principal components (PC₁, PC₂, and PC₃) in the stable conditions and in the three tests in unstable conditions: *PRE* - before practice, *MID* - in the middle of the practice, *POST* - after practice.

Table 2
The number of occurrences of different M-modes

M-modes Pattern	Conditions			
	STABLE	PRE	MID	POST
Reciprocal				
Push-back	12	5	5	9
Push-forward	8	3	2	5
Co-contraction				
Hip	2	1	0	2
Knee	0	4	0	0
Ankle	0	1	0	1
Mixed				
Mix1	1	4	2	0
Mix2	0	1	1	1
Mix3	0	0	2	2
Mix4	0	5	5	2
Mix5	0	0	1	1
Singular	1	0	6	1

Data across all subjects are presented. *STABLE* - under the stable condition, *PRE* - before practice, *MID* - in the middle of the practice, *POST* - after practice under the unstable condition, *Singular* - one muscle loaded significantly on a mode.