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Multi-Muscle Synergies in an Unusual Postural Task:

Quick Shear Force Production

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Abstract

We considered a hypothetical two-level hierarchy participating in the control of vertical posture. The framework of the uncontrolled manifold (UCM) hypothesis was used to explore the muscle groupings (M-modes) and multi-M-mode synergies involved in stabilization of a time profile of the shear force in the anterior-posterior direction. Standing subjects were asked to produce pulses of shear force into a target using visual feedback while trying to minimize the shift of the center of pressure (COP). Principal component analysis applied to integrated muscle activation indices identified three M-modes. The composition of the M-modes was similar across subjects and the two directions of the shear force pulse. It differed from the composition of M-modes described in earlier studies of more natural actions associated with large COP shifts. Further, the trial-to-trial M-mode variance was partitioned into two components: one component that does not affect a particular performance variable (V_{UCM}), and its orthogonal component (V_{ORT}). We argued that there is a multi-M-mode synergy stabilizing this particular performance variable if V_{UCM} is higher than V_{ORT} . Overall, we found a multi-M-mode synergy stabilizing both shear force and COP coordinate. For the shear force, this synergy was strong for the backward force pulses and non significant for the forward pulses. An opposite result was found for the COP coordinate: the synergy was stronger for the forward force pulses. The study shows that M-mode composition can change in a task-specific way and that two different performance variables can be stabilized using the same set of elemental variables (M-modes). The different dependences of the ΔV indices for the shear force and COP coordinate on the force pulse direction supports applicability of the principle of superposition (separate controllers for different performance variables) to the control of different mechanical variables in postural tasks. The M-mode composition allows a natural mechanical interpretation.

Keywords

synergy; posture; muscle mode; uncontrolled manifold hypothesis; electromyogram; reference configuration hypothesis

INTRODUCTION

The notion of multi-muscle synergies has been invoked in many studies of postural tasks (Krishnamoorthy et al. 2003a,b, 2004; Ivanenko et al. 2005, ²⁰⁰⁶; Ting and Macpherson 2005; Wang et al. 2005, 2006; Torres-Oviedo et al. 2006; Danna-Dos-Santos et al. 2007) as a means of reducing (but not eliminating) the notorious redundancy of the multi-muscle system (cf. Bernstein 1967). In a series of recent studies, the framework of the uncontrolled manifold (UCM) hypothesis has been used to quantify multi-muscle synergies involved in various tasks such as preparation to a self-inflicted postural perturbation (Krishnamoorthy et al. 2003b),

preparation to making a step (Wang et al. 2005, 2006), and voluntary sway (Danna-Dos-Santos et al. 2007). The UCM hypothesis (Scholz and Schüner 1999; reviewed in Latash et al. 2002b, 2007) assumes that the neural controller acts in a space of elemental variables, forms in that space a sub-space (UCM) corresponding to a desired value (time profile) of an important performance variable, and then confines most of the variability to that sub-space. If most of the trial-to-trial variance is confined to the UCM, a conclusion can be drawn on a synergy among the elemental variables *stabilizing* the performance variable (i.e., decreasing its variability across trials). In this context, the term *stabilization* does not refer to the classical mechanical concept of stability, but to reproducibility of a performance value (or of its time profile) over successive trials.

Application of the UCM framework to multi-muscle synergies has been based on the assumption that control of such synergies is based on a two-level hierarchy. At the lower level, muscles form groups, within which their levels of activation co-vary across a wide range of tasks. Such groups have been referred to as muscle modes (M-modes, Krishnamoorthy et al. 2003a,b) or muscle synergies (Ivanenko et al. 2004, 2005, 2006; Ting and Macpherson 2005; Torres-Oviedo and Ting 2007; Saltiel et al. 2001; D'Avela et al. 2005). At the upper level, the M-modes are considered as the elemental variables, and their co-variation is organized in a task-specific manner to stabilize an important performance variable. The idea of a two-level hierarchy has been supported by studies that showed similar M-modes but different multi-M-mode co-variation indices across different tasks and subjects (Krishnamoorthy et al. 2003a; Danna-Dos-Santos et al. 2007) and also by reports of changes in the M-mode composition in unusual conditions (Krishnamoorthy et al. 2004) and with practice (Asaka et al. 2007).

Most earlier studies of M-mode synergies in postural tasks focused on stabilization of the trajectory of the center of pressure (COP, the point of application of the resultant vertical force acting on the body from the supporting surface). Indeed, the COP shifts have been traditionally viewed as crucial for postural control (Winter et al. 1996). However, another component of the external forces applied to the ground also has an important contribution to postural stability, that is, the shear force. Indeed, shear force at the level of the support surface does not affect the COP location but is mechanically linked to acceleration of the center of mass of the body. A number of studies investigated EMG patterns in response to a sudden surface translation (Horak and Nashner 1986, Henry et al. 1998, Torres-Oviedo and Ting 2007). In those studies, shear force changes were produced by the subjects but they were not explicit task components, rather the means to restore balance. To our knowledge, no quantification of the M-mode synergies has been performed in shear force production tasks.

In the current study, we explored multi-muscle synergies involved in stabilization of the shear force time profile in the anterior-posterior direction. This required the performance of a rather unusual task by the subjects: to produce pulses of shear force into a target, using visual feedback, while trying to minimize the shift of the center of pressure (COP). At the lower level of the hypothetical control hierarchy, we expected the subjects to form a set of muscle modes that would differ from those described in earlier studies of more natural actions associated with large COP shifts. We expected the M-mode composition to be similar across subjects and directions of the force pulse. At the higher level of the hierarchy, we expected the subjects to show co-variation of the M-mode involvement across trials to stabilize a time profile of the shear force or, in other words, to show multi-M-mode force-stabilizing synergies. We also explored whether the same set of M-modes could be involved in stabilization of the COP shifts.

METHODS

Participants

Eight subjects, 4 males and 4 females, took part in the experiments. Their mean age was 28 years (SD 3.4), mean height was 1.71 m (SD 0.09) and mean weight was 70 kg (SD 20). All subjects were healthy, without any known peripheral or neurological disorder. All the subjects gave their informed consent according to the procedures approved by the Office of Research Protection of the Pennsylvania State University.

Apparatus

A force platform (AMTI, OR-6) was used to measure the moments of force about the central frontal and sagittal axes of the platform (M_Y and M_X , respectively) and the three components of the reaction force, F_X - in the anterior-posterior direction, F_Y - in the medio-lateral direction, and F_Z - vertical.

Disposable self-adhesive electrodes (3M Corporation) were used to record the surface muscle activity (EMG) of the following muscles: soleus (SOL), gastrocnemius lateralis (GL), gastrocnemius medialis (GM), tibialis anterior (TA), biceps femoris (BF), semitendinosus (ST), rectus femoris (RF), vastus medialis (VM), lumbar erector spinae (ES), and rectus abdominis (RA). The electrodes were placed on the right side of the subject's body over the muscle bellies. The distance between the two electrodes of each pair was 3 cm. The signals from the electrodes were pre-amplified (x 3000) and band pass filtered (60-500 Hz). All the signals were sampled at 960 Hz with a 12-bit resolution. A personal computer (Gateway 450 MHz) was used to control the experiment and to collect the data using the customized LabView-based software (LabView-8, National Instruments, Austin, TX, USA).

Procedures

The subjects were asked to stand quietly on the force platform with the feet parallel to each other spaced by 20 cm. There were several series with the shear force pulse production and three control trials. Except for the two control trials with holding a load, the subjects were instructed to keep their arms crossed on the chest (Figure 1b).

The experiment began with three control trials, later used for the EMG normalization. The first of these trials involved 30 s of quiet standing. In two other trials, the subjects were instructed to stand quietly and hold a standard load (5 kg) for 15 s in front of the body keeping the arms fully extended. The subjects held the load by pressing on two circular panels attached to the ends of a bar. The load was either suspended from the middle of the bar or it was attached through a pulley system such that it produced an upward acting force on the bar (Figure 1a). Across all the control trials, the subjects were instructed to maintain their center of mass (COM) at the same location. A monitor located 0.8 m from the subject at the eye level was used to provide visual feedback on the location of the projection of the COM onto the X axis, approximated from the torque equilibrium static equation (see Figure 1a):

$$X_{CoM} = \frac{-M_Y - m_{load} \cdot g \cdot X_{Load}}{m_{body} \cdot g}$$

where:

M_Y : the moment of force measured by the platform (i.e. applied by the subject to the ground).

m_{load} : mass of the load.

X_{load} : coordinate of the load with respect to the trunk. In a first approximation, X_{load} was approximated as the arm length, measured with the arms horizontal from the acromion to the third metacarpophalangeal joint.

m_{body} : mass of the subject. g : gravity acceleration, 9.81 m/s^2 .

During the shear force production task, subjects were given two visual feedback signals on the same monitor: the shear force in the anterior-posterior direction (F_X) in newtons and the transversal torque (M_Y) in newton-meters. The y scales were identical for both variables (-150 to +150). Subjects were instructed to produce pulses of F_X into a target shown by a horizontal line on the monitor, while trying their best to keep M_Y constant. Three levels of force (60 N, 90 N and 120 N) in both directions (forward and backward) were used as targets. In the following, the term “experimental condition” will refer to the six different combinations of these two factors. For each experimental condition, five successive trials of 30 seconds each were recorded. During each trial, the subjects produced several force pulses to the same target. The pulses were self-paced, and subjects were instructed to stabilize their posture (i.e. make F_X zero) between trials. In pilot trials, we verified that one second was sufficient to stabilize F_X at zero level after a force pulse. On average, subjects performed between 10 and 20 pulses per trial. The time interval between trials was 30 seconds. The fifteen trials (5 trials * 3 force targets) for a given pulse direction were performed in a block. For practical reasons, mainly to avoid effects of fatigue that could be expected from the high force target trials, the three force targets were presented in an increasing order. Note that the different targets were used to produce enough spread of the data to compute the muscle modes, not to study the effect of this factor. The order of the two blocks (forward or backward pulses) was presented in a balanced order. There were at least 5 min rest intervals between the blocks to avoid fatigue.

At least three practice trials of 30 s each were performed by the subjects before each block. In addition, before each new experimental condition, subjects were permitted to practice the task as many times as needed until they were comfortable with it. The amount of this additional practice time varied among subjects, but it was always under two minutes.

In the following text, we use the following convention: the direction of the pulse corresponds to the direction of the initial acceleration of the body COM. For example, a “backward pulse” corresponds to an acceleration of the COM backward, and thus to a forward (positive) force produced by the subject on the platform (F_X).

Data Processing

All signals were processed off-line using the Matlab 7.3 software package. Typical F_X time profiles represented a sequence of pulses in opposite directions, which allowed decelerating the COM and restoring balance (Figure 2a). Only the first force pulse (in the required direction) was analyzed. The EMG and mechanical data were analyzed as follows (cf. Figure 2a):

1. F_X was filtered with a 20-Hz low-pass second-order zero-lag Butterworth filter and numerically differentiated twice;
2. The first peak of d^2F_X/dt^2 was detected within the 200 ms window prior to the F_X peak;
3. The beginning of the pulse (t_0) was defined at the time when d^2F_X/dt^2 exceeded 5% of the d^2F_X/dt^2 peak value;
4. The end of the pulse (t_{end}) was defined as the time when F_X changed its sign after reaching a peak;
5. An additional period of 2/3 of the pulse duration ($t_{end} - t_0$) was analyzed before t_0 . The total time window will be addressed as “analysis time” (T_{AN}).

6. In order to analyze data across pulses, they were time normalized by the analysis time (T_{AN}) and re-sampled over one hundred points. For further analysis, 10 time windows of equal duration (10 % of the pulse duration) were used.

For each of the six experimental conditions subjects performed between 50 and 90 pulses. For further analyses, only the 20 “best” pulses were analyzed. They were selected based on the following index of performance I_{perf} :

$$I_{perf} = 100 * \frac{|\varepsilon_{F_X}| + c * |\varepsilon_{M_Y}|}{|F_{TARGET}|}$$

with:

ε_{F_X} : difference between the target and the peak of F_X (in N);

ε_{M_Y} : maximal difference between M_Y and its initial value over the period considered (in Nm);

c : coefficient (in m^{-1}) to match the units of ε_{F_X} and ε_{M_Y} ($c = 2 m^{-1}$, pilot tests showed that the influence of c magnitude was small);

$|F_{TARGET}|$: the absolute value of the shear force target (in N).

This index reflects by how much the subjects missed the F_X target, and how much M_Y varied. Thus, smaller values of this index correspond to better performance. Twenty pulses with the lowest values of I_{perf} were accepted for each condition. An additional visual inspection allowed rejecting aberrant pulses (about 2% of the accepted pulses).

In order to check the potential linear relations between the time profiles of F_X and M_Y produced by the subjects, these time profiles were averaged across subjects for each experimental condition and submitted to a cross-correlation analysis. This analysis was run over 90 points of the analysis time window (from 10% to 100%); 101 lag values between $F_X(t)$ and $M_Y(t)$ were considered (from -50 to +50).

EMG signals were rectified and filtered using a low-pass second-order zero-lag Butterworth filter with a cut-off frequency of 50 Hz. For the control trials, the rectified EMG signals were averaged over a 5-s period of time selected in the middle part of the trial. For the main trials, the rectified EMG signals were integrated over 10% time windows ($IEMG$), and normalized using the method previously described by Krishnamoorthy et al. (2003a):

$$IEMG_{norm} = \frac{IEMG - IEMG_{qs}}{IEMG_{ref}}$$

where:

$IEMG_{qs}$: average rectified EMG obtained during the quiet standing trial integrated over a time window of the same duration as $IEMG$ was;

$IEMG_{ref}$: average rectified EMG obtained during the two control trials with holding a load integrated over a time window of the same duration as for $IEMG$. For the dorsal muscles (SOL, GM, GL, BF, ST), this value is computed using the data from the control trial where the load was acting downward. For the frontal muscles (TA, RF, VM, RA), this value is computed using the data from the control trial where the load was acting upward.

Defining M-modes

The objective of this step was to define the groups of muscles (muscle modes or M-modes) that co-varied across tasks with different magnitudes of the shear force pulse. Sets of such groups were further used as the sets of elemental variables for the UCM analysis. Their identification reduced the 10-dimensional muscle activation space to a 3-dimensional M-mode space.

For each subject and each direction of pulse, the $600 * 10 IEMG_{norm}$ correlation matrix (10 time windows * 20 pulses * 3 targets; 10 muscles) was subject to PCA, using the Matlab 7.3 software. For PCs accounting for more than 10% of the variance, the factor loadings were subjected to Varimax rotation. Visual inspection of the scree plots confirmed the validity of this criterion. For each data set, we found that each of the first three PCs accounted for more than 10% of the variance before rotation. This is consistent with previous studies using the same method but a different criterion (Krishnamoorthy et al. 2003a,b). Thus, for each time windows, the integrated activation of the ten recorded postural muscles can be described in the M-mode space by only three parameters, namely the magnitudes of the three M-modes. These magnitudes are obtained by multiplying the *IEMG* values by the loadings of the M-modes after Varimax rotation. The amounts of variance explained after rotation by these first three PCs were then z-transformed and subjected to one-way ANOVAs with factors *Subject* and *Direction* (two levels, forward and backward) respectively.

To test the hypothesis that the M-modes were similar across subjects and directions of the pulse, we used the concept of a central vector, previously described by Krishnamoorthy et al. (2003a). The general idea is to compare the similarity between the directions of several vectors in the muscles space and the direction of a central vector representing either the same group of vectors or another group of vectors. The central vector is analogous to the mean vector. We used the cosine of the angle between the central vector and each of the individual PC vectors to estimate the similarity of their directions.

For each of the three PCs, two direction-specific central vectors (one for each direction) $C_i(d)$ ($i=1 \rightarrow 3$, $d=1 \rightarrow 2$) were identified across the 8 subjects, and eight subject specific central vectors (one for each subject) $C_i(s)$ ($i=1 \rightarrow 3$, $s=1 \rightarrow 8$) were identified across the two directions. Cosines of angles between each $C_i(s)$ and the M-modes vectors M_j ($j=1 \rightarrow 3$) for each subject and each direction were computed. The cosines of angles between each $C_i(d)$ and the M_j vectors for each subject and each direction were also computed. These cosines were transformed into z-scores, using Fisher's z-transformation. Statistical analyses were further performed on the z-scores.

We assume that the PC directions are similar across subjects if for each $C_i(d)$, the z-scores of the cosines obtained between the $C_i(d)$ and the M_j are significantly higher for $i=j$ as compared to $i \neq j$. We also assume that the PCs are similar across directions if for each $C_i(s)$, the z-scores obtained between the $C_i(s)$ and the M_j are significantly higher if $i=j$ as compared to $i \neq j$. Two-way ANOVAs with factors *Mode* (M1, M2, M3) and *Direction* (forward and backward), and *Mode* and *Subjects* (eight levels) were run on the z-scores computed for each of the three P_i . Tukey's post-hoc tests were used to analyze the significant effects.

Defining the Jacobian

The objective of this step was to define the relations between small changes in the magnitudes of the elemental variables (the M-modes defined in the previous step) and changes in a performance variable. Note that this analysis is performed at the higher level of the assumed control hierarchy, where not the EMG activities of individual muscles but the M-modes are

treated as elemental variables. These relations were assumed linear, and thus were expressed using a Jacobian matrix:

$$\Delta PV = k_1 \cdot \Delta m_1 + k_2 \cdot \Delta m_2 + k_3 \cdot \Delta m_3 = \mathbf{J} \Delta \mathbf{m}^T$$

Where:

ΔPV is the changes in a performance variable;

$\mathbf{J} = [k_1 \ k_2 \ k_3]$ is the Jacobian matrix reduced in this case to a line vector;

$\Delta \mathbf{m} = [\Delta m_1 \ \Delta m_2 \ \Delta m_3]$ is the 3 by 1 vector of change in the M-mode magnitudes.

Assuming such a linear relation is an oversimplification of the problem of linking muscle activation indices to changes in the endpoint force and its coordinate. However, as in earlier studies (Krishnamoorthy et al. 2003b; Wang et al. 2005; Danna-Dos-Santos et al. 2007), this simple model led to statistically significant relations between changes in the M-mode magnitudes and performance variables (see Results).

Changes in the magnitude of the M-modes (computed as the sum of the products of the muscle activation indices and corresponding factor loadings) were computed between two consecutive 10% time windows. In this study, two performance variables were investigated: the shear force F_X and the transversal torque M_Y . A time lag was assumed between changes in the electrical elemental variables and the mechanical performance variable, the electromechanical delay (cf. Corcos et al. 1992). The magnitude of the electromechanical delay was estimated as described later.

Multiple linear regression was used to compute the k coefficients for each of the eight subjects, the six experimental conditions, the two performance variables and five different time lags (from 0 time windows to 4 time windows) separately.

For the two performance variables, the influence of the time lag on the total amount of variance explained by the multiple linear regression was investigated using a one-way ANOVA with the factor *Lag* on the z-transformed R^2 values. The lag value corresponding to the maximal variance accounted for was accepted as the optimal lag (i.e., optimal estimate of the electromechanical delay). All further analyses were performed using this optimal lag value.

The influence of the direction of pulse and of the force target level on the amount of variance accounted for by the linear model was investigated with a two-ways ANOVA with factors *Direction* and *Target* performed on the z-transformed R^2 . For each of the two performance variables, a paired Student's t-test was performed on the z-transformed R^2 to check the difference of variance explained between the forward and backward force pulses.

Uncontrolled manifold (UCM) analysis

Within the UCM analysis, we partitioned the trial to trial variance in the changes of the elemental variables (M-modes) into two components. The first component lies within a sub-space (the UCM) that does not affect a selected performance variable (F_X or M_Y). In a linear approximation, this sub-space was computed as the null-space of the Jacobian matrix $\mathbf{J}$ defined at the previous step. The other component of the variance lies within an orthogonal complement to the UCM. The comparison of the two components of the variance, normalized by the dimensionality of their respective sub-spaces, is a way to quantify the amount of variance that is compatible with stabilization of the selected performance variable (i.e. to quantify the strength of the multi-muscle synergy stabilizing this performance variable).

This analysis was performed for each subject, each of the six experimental conditions, and the two performance variables (F_X and M_Y), using the Jacobian matrices obtained at the optimal time lag, as follows:

1. Computation of the null space. The space of the elemental variables is three-dimensional. For a one-dimensional performance variable (F_X or M_Y), the null-space of $\mathbf{J}$ is two-dimensional. The basis vectors $\mathbf{e}_1$ and $\mathbf{e}_2$ defining this plane were computed using a Singular Value Decomposition of the $\mathbf{J}$ matrix.
2. Computation of the trial-to-trial variance of the changes in the M-mode magnitudes between each pair of consecutive 10% time windows for each experimental condition and each subject. The changes in the mode magnitudes were averaged across the twenty pulses. For every pulse, this averaged vector $\bar{\Delta\mathbf{M}}$ was subtracted from the vectors of the individual changes in the mode magnitudes $\Delta\mathbf{M}$:

$$\Delta\mathbf{M}_{\text{demeaned}} = \Delta\mathbf{M} - \bar{\Delta\mathbf{M}}.$$

3. Projection of these individual residual mean-free vectors ($\Delta\mathbf{M}_{\text{demeaned}}$) onto the UCM (vector $\mathbf{f}_{\text{UCM}}$) and the orthogonal subspace (vector $\mathbf{f}_{\text{ORT}}$):

$$\mathbf{f}_{\text{UCM}} = \sum_{i=1}^2 \mathbf{e}_i^T \cdot \Delta\mathbf{M}_{\text{demeaned}} \cdot \mathbf{e}_i$$

$$\mathbf{f}_{\text{ORT}} = \Delta\mathbf{M}_{\text{demeaned}} - \mathbf{f}_{\text{UCM}}$$

4. Computation of the total trial-to-trail variance (V_{TOT}) and of the components of this variance in each of the two subspaces (V_{UCM} and V_{ORT}), normalized per degree-of-freedom of the respective subspace (3, 2 and 1 for V_{TOT} , V_{UCM} and V_{ORT} , respectively):

$$V_{TOT} = \sigma_{TOT}^2 = \frac{1}{3 * N_{\text{trial}}} \sum_{i=1}^{N_{\text{trial}}} \|\Delta\mathbf{M}_{\text{demeaned}}\|^2$$

$$V_{\text{UCM}} = \sigma_{\text{UCM}}^2 = \frac{1}{2 * N_{\text{trial}}} \sum_{i=1}^{N_{\text{trial}}} \|\mathbf{f}_{\text{UCM}}\|^2$$

$$V_{\text{ORT}} = \sigma_{\text{ORT}}^2 = \frac{1}{N_{\text{trial}}} \sum_{i=1}^{N_{\text{trial}}} \|\mathbf{f}_{\text{ORT}}\|^2$$

5. Computation of an index of synergy, ΔV , to quantify the relative amount of variance that is compatible with stabilization of the selected performance variable. We normalized the index by the total amount of variance similarly to how this was done in earlier studies (Krishnamoorthy et al. 2003b; Danna-Dos-Santos et al. 2007):

$$\Delta V = \frac{V_{UCM} - V_{ORT}}{V_{TOT}}$$

The influence of the direction of pulse on the total variance V_{TOT} , such as the evolution of V_{TOT} along the time of analysis, are investigated through a two-ways ANOVA performed on the logarithmic transformation on V_{TOT} with factors *Time Windows* (1-2 → 7-8) and *Direction* (forward and backward). Another analysis was run on the differences between variances observed for the forward and backward force pulses, computed for the two components of the variance (V_{UCM} and V_{ORT}), the two performance variables (F_X and M_Y), the seven time windows (1-2 → 7-8) and the eight subjects. To observe the effect of different factors on these differences, they were submitted to a three-ways ANOVA with factors *Time Windows* (1-2 → 7-8), *Performance Variable* (F_X and M_Y) and *Variance Component* (V_{UCM} and V_{ORT}).

Since V_{UCM} , V_{ORT} and V_{TOT} are computed per degree-of-freedom, the index of synergy ΔV ranges between 1.5 (all variance is within the UCM) and -3 (all variance is in the orthogonal sub-space). For statistical analysis, the ΔV indexes were transformed using a Fisher's z-transformation adapted to the boundaries of ΔV :

$$z_{\Delta V} = .5 * \text{Log} \left(\frac{3 + \Delta V}{1.5 - \Delta V} \right)$$

One sample Student's t-tests were performed on these z-scores averaged across subjects, Time Windows, and targets to check if they were significantly different from $.5 * \text{Log}(2)$ (i.e. ΔV significantly different from zero). Bonferroni corrections were used to reflect the multiple comparisons. A three-ways ANOVA was performed on $z_{\Delta V}$ with factors *Time Window* (1-2 → 7-8), *Performance Variable* (F_X and M_Y) and *Direction* (forward and backward).

RESULTS

General performance

All eight subjects were able to perform the task successfully: On average, they reached the force target accurately, without producing a large change in the transversal torque. At the time of the peak force for the highest force target (120 N), the maximal observed change in M_Y was 20 Nm (corresponding to about 3 cm of COP displacement). The top two panels of Figure 3 shows an example of the time profiles of F_X and M_Y recorded for the highest target level (120 N), and averaged across trials for a typical subject. The bottom panels show the same variables averaged across trials and then across subjects. The dotted lines represent plus or minus the standard deviation across subjects. Note that the variability across trials and across subjects remained small. The average duration of the force pulses was 192 ms corresponding to the average analysis time (T_{AN}) of 288 ms.

The time profiles $F_X(t)$ and $M_Y(t)$ averaged across trials and subjects within each experimental condition were submitted to cross-correlation analysis (cf. Method). Table 1 shows the squared correlation coefficients when no lag was introduced between $F_X(t)$ and $M_Y(t)$ (R^2_{0lag}) as well as the maximum correlation coefficients (R^2_{max}) and the associated lag in percentage of T_{AN} . For the forward force pulses, the subjects showed only weak correlations between $F_X(t)$ and $M_Y(t)$ at zero lag. The peak values of R^2_{max} were under 0.62 and these peak values were reached at substantial delays between the two mechanical variables. In contrast, the correlation

coefficients between $F_X(t)$ and $M_Y(t)$ for the backward force pulses were high (over 0.95), and their peak values were reached close to zero time lag (within 2% of T_{AN}).

Figure 4 presents an example of the EMG time profiles averaged across 20 pulses for a typical subject, for the highest force target value and for both force pulse directions. Typical EMG patterns involved a sequence of bursts in the dorsal and ventral muscles more prominent in the proximal muscle groups. For the forward force pulses, the first EMG burst could be seen in the activity of tibialis anterior (TA), biceps femoris (BF), semitendinosus (ST), and erector spinae (ES). For the backward pulses, the first burst was observed in the EMG signals of rectus femoris (RF), vastus medialis (VM), and rectus abdominis (RA).

Muscle modes

The EMG profiles, were subjected to the principal component analysis (PCA), run on the normalized integrated EMG indices ($IEMG_{NORM}$) computed over ten time windows, each equal to 10% of the total time of analysis (see Methods for details). For each subject and each direction of pulse, the PCA resulted in three PCs that accounted for more than 10% of the total variance each. On average, the amounts of variance explained by the first three PCs after rotation were 29.4%, 23.8% and 21.3%, respectively, i.e. these three PCs accounted on average for 74.5% of the total variance.

Table 2 shows the PCA loadings averaged across subjects. Table 3 shows the number of subjects for whom the loading of a given muscle in a given PC was over 0.5. In both Tables, the high loadings and occurrences are shown in bold for each muscle and the two directions of force production. The following three groups of muscles or (muscle modes, M-modes) were identified:

- M_1 , composed of the dorsal muscles of the thigh and the trunk and, sometimes, the ankle dorsiflexor: BF, ST, ES, and TA;
- M_2 composed of the ventral muscles of the thigh and the trunk: RF, VM, and RA;
- M_3 composed of the muscles forming the triceps surae group: SOL, GL, and GM.

Note that the $IEMG$ indices for some muscles, such as TA and RA, showed more variability in the loading coefficients across subjects. In some subjects, these muscles could be represented in different M-modes. Besides, lower absolute values of the loading coefficients and higher indices of their variability were seen during backward force pulses as compared to the forward force pulses. To check the similarity of the M-modes across subjects and directions, the method proposed by Krishnamoorthy et al. (2003a) based on the central vector concept was used (see Methods for details). The method compares the similarity between the directions of several vectors in the muscles space and the direction of a central vector of either the same group of vectors or another group of vectors. We used the cosine between two vectors as a measure of similarity in their directions. Further, the cosine values were transformed into z-scores. Figure 5 displays the z-scores averaged across subjects and force pulse directions. Note that the scores were much higher for pairs of vectors composed of a central vector and an M-mode of the same number, for example P_1 and M_1 , P_2 and M_2 , and P_3 and M_3 , as compared to pairs composed of vectors of different numbers (for example, P_1 and M_3).

These results were confirmed by two-way ANOVAs run across subjects and across directions separately:

- For each central vector, a two-way ANOVA with factors *Mode* (M_1 , M_2 , M_3) and *Direction* (forward and backward) was run on the z-scores of the cosines computed between the central vectors and M-modes across subjects. It showed a significant effects of *Mode* ($F_{(2,42)} > 90$, $P < 0.001$). No significant interactions were found.

Tukey's post-hoc test showed that the z-score between M-modes M_j and the central vectors $P_i(d)$ were significantly higher if $i = j$ as compared to $i \neq j$ ($p < 0.001$).

- For each central vector, a two-way ANOVA with factors *Mode* (M_1, M_2, M_3) and *Subject* ($S_1 \rightarrow S_8$) was run on the z-scores of the cosines computed between the central vectors and M-modes across directions. It showed that *Mode* was the only significant factor ($F_{(2,24)} > 49, P < 0.001$). There was a significant interaction *Subject* $\times$ *Mode* for the central vector P_2 only [$F_{(14,24)} = 4.51, P < 0.001$]. Tukey's post-hoc test confirmed that the z-score between the M-modes M_j and the central vectors $P_i(s)$ were significantly higher if $i = j$ as compared to $i \neq j$ ($p < 0.001$).

These results indicate that the individual M-Modes M_i were clustered around their respective central vectors P_i . They confirm the similarity of the M-modes across subjects and directions.

Definition of the Jacobians

Linear relations between small changes in the magnitude of muscle modes (ΔM) and small changes in performance variable (ΔPV) were assumed and expressed using the Jacobian matrix (see Methods). The changes in the magnitude of M-modes were computed between each two consecutive 10% time windows. Different time lags between the M-mode changes and the performance variables (F_X and M_Y) changes were introduced to estimate the electromechanical delay. The coefficients of multiple linear regression were computed for each of the eight subjects, each of the six experimental conditions, each of the two performance variables, and five different time lags (from 0 time windows to 4 time windows) separately.

The percentage of variance accounted for by the linear regression (R^2) showed a significant dependence on the time lag. This has been confirmed for both F_X and M_Y , with one-way ANOVAs with the factor *Lag* performed on the z-transformed R^2 values [$F_{(4,235)} > 5.0, p < 0.001$]. The highest amount of variance explained was obtained for a lag of two time windows (57 ms on average). For this time lag, changes in the M-mode magnitudes explained, on average, 59.0% of the change in F_X and 47.9% of the change in M_Y . All the following analyses were performed using the data at this optimal time lag.

An example of the changes in the M-mode magnitudes between successive time windows, averaged across force pulses and subjects, for the medium target and the two directions of shear force pulses, is shown in Figure 6. Note the similar time evolutions of M_2 and M_3 , although sometimes with a short time lag; M_1 showed a substantially different time profile.

Figure 7 illustrates, for both performance variables, the influence of the direction of force pulse on the amount of variance explained by the linear regression between the changes in M-modes and the changes in the performance variables. For F_X , the amount of variance was higher for the forward pulses (66.1% of the total variance) than for the backward pulses (51.9% of the total variance). In contrast, for M_Y , the amount of variance explained was smaller for the forward pulses (43.5%) than for the backward pulses (52.3%). This difference was only significant for F_X , as confirmed by one-way ANOVA with the factor *Direction* on the z-transformed R^2 values. There was a significant effect of *Direction* for F_X [$F_{(1,46)} = 10.47, p < 0.05$] but only a close to significant effect for M_Y [$F_{(1,46)} = 2.93, p = 0.09$].

UCM analysis

The UCM analysis was used to quantify two components of the trial-to-trial variance of the changes in time of the M-mode magnitudes, one that does not affect a selected mechanical variable, F_X or M_Y , (V_{UCM}) and the other that does (V_{ORT}). The total variance (V_{TOT}) was computed between each pair of consecutive 10% time windows across 20 pulses (for each experimental condition and each subject separately). Note that, due to the introduction of the

time lag between the muscle activations and the mechanical variables (see earlier), the analysis was performed over eight time windows (see Methods and Figure 2B). An index of synergy (ΔV) was used to quantify the relative amount of V_{UCM} in V_{TOT} such that positive values of ΔV corresponded to stabilization of the selected performance variable by co-varied adjustments in the M-mode magnitudes across trials.

Figure 8 illustrates time changes in V_{TOT} , averaged across subjects and force targets. Note an increase in V_{TOT} during the force pulse (after the time windows #3). Note also that V_{TOT} was higher for the backward pulses than for the forward pulses. This was confirmed with a two-ways ANOVA performed on the log-transformed V_{TOT} with factors *Time Window* (1-2 $\rightarrow$ 7-8) and *Direction* (forward and backward). It showed a significant effect of both factors, *Time Window* [$F_{(6,322)} = 106.5$, $p < 0.001$] and *Direction* [$F_{(1,322)} = 44.2$, $p < 0.001$], as well as a significant interaction between these two factors [$F_{(1,322)} = 3.58$, $p < 0.05$].

Partitioning V_{TOT} into V_{UCM} and V_{ORT} showed different patterns for the analyses performed for F_X and M_Y . Figure 9 shows the time evolution of the two variance components, V_{UCM} and V_{ORT} , averaged across subjects and targets, for both F_X and M_Y and the two pulse directions. These graphs highlight the differences between the forward and backward pulses. In particular, for F_X , V_{UCM} for the backward pulses was higher than for the forward pulses, while V_{ORT} showed little difference between the forward and backward pulses. An opposite pattern can be seen for M_Y : V_{UCM} is almost the same for both force pulse directions, while V_{ORT} is higher for the backward pulses. The mentioned differences are particularly pronounced during the pulse time (after the time window #3). These results were supported by the following statistical analysis. The difference between the variance indices for the forward and backward pulses were computed for the two components of the variance (V_{UCM} and V_{ORT}), the two performance variables (F_X and M_Y), the seven time windows (1-2 $\rightarrow$ 7-8), and the eight subjects. These indices were submitted to a three-ways ANOVA with factors *Time Window* (1-2 $\rightarrow$ 7-8), *Performance Variable* (F_X and M_Y) and *Variance Component* (V_{UCM} and V_{ORT}). It showed a significant effect of *Time Window* [$F_{(6,644)} = 4.18$, $p < 0.001$] and significant interactions *Performance Variable* $\times$ *Variance Component* [$F_{(1,644)} = 25.7$, $p < 0.001$] and *Time Windows* $\times$ *Performance Variable* $\times$ *Variance Component* [$F_{(6,644)} = 2.86$, $p < 0.05$]. The first interaction confirms that the effect of the performance variable on the difference of variance indices between the forward and backward pulses depended significantly on the variance component, i.e. for F_X these differences appeared mainly for V_{UCM} , while for M_Y they were seen mainly for the V_{ORT} . The second interaction reflects the fact that this effect was statistically more pronounced for the time windows during the pulse production.

Figure 10 presents the index ΔV , reflecting the normalized difference between V_{UCM} and V_{ORT} (see Methods), averaged across subjects, for different time windows, both experimental conditions and both performance variables. Figure 11A shows the same index averaged across subjects, targets and time windows, while Figure 11B shows this index averaged across subjects, targets and direction of pulses.

The first observation is that ΔV values are predominantly positive (see Figure 11A). One sample t-tests were performed on the z-transformed ΔV averaged across subjects, time intervals and force targets. Bonferroni corrections were applied to reflect the multiple comparisons. The results confirmed that the averaged ΔV indexes were significantly positive ($p < 0.0125$) for M_Y for both direction of force pulses, and for F_X for the backward force pulses, but not for the forward force pulses.

On average, ΔV was higher for the backward pulses than for the forward pulses (Figure 11B). This difference was seen mainly before time window #4, i.e. during the preparation to the pulse and at its very early phase.

Effects of the force pulse direction on ΔV were opposite for the two performance variables. For the backward pulses, consistently positive values of ΔV for F_X were observed (>0.47), while for the forward pulses, this index was low (grand average of 0.15); results for M_Y were almost opposite, higher positive values of ΔV were observed for the forward force pulses.

These results were statistically confirmed by a three-way ANOVA performed on the z-transformed ΔV values with factors *Time Window* (1-2 $\rightarrow$ 7-8), *Performance Variable* (F_X and M_Y) and *Direction* (forward and backward). There was a significant effect of *Direction* [$F_{(1,644)} = 6.79$, $p < 0.001$] and two significant interactions: *Direction* $\times$ *Time Window* ([$F_{(6,644)} = 3.37$, $p < 0.05$]) and *Direction* $\times$ *Performance Variable* ([$F_{(1,644)} = 53.58$, $p < 0.001$]). These results reflect the fact that ΔV was, overall, significantly higher for the backward pulses than for the forward pulses, and that this difference varied over the time of analysis (interaction *Direction* $\times$ *Time Window*). It also confirms that the influence of the direction of pulse on ΔV was different for the two performance variables (interaction *Direction* $\times$ *Performance Variable*).

DISCUSSION

Two hypotheses have been formulated in the Introduction. They are related to the composition of muscle groups (M-modes) and their co-variation computed with respect to an average across trials time profile of the shear force (F_X) in the anterior-posterior direction. The results have supported both the first hypothesis that the M-mode composition would differ from that reported for studies with controlled COP displacement (e.g., Danna-Dos-Santos 2007) and the second hypothesis that the M-modes would co-vary across trials such that most of the trial-to-trial variance in the M-mode space lies in a subspace where it does not affect the shear force magnitude. These results and their implications for the hierarchical control of multi-muscle systems in general, and for the control of postural tasks in particular, are discussed in the following sections.

Composition of muscle modes

Three M-modes represented linear combinations of activation indices for the ten leg/trunk muscles. The modes were similar across subjects and the two directions of shear force; however, their composition in the current study was different as compared to earlier studies of postural tasks that required large COP shifts (Krishnamoorthy et al. 2003b; Wang et al. 2005; Danna-Dos-Santos et al. 2007). In particular, the triceps surae muscle group formed its own M-mode rather than join other major dorsal muscles in a common M-mode. In addition, tibialis anterior frequently was part of an M-mode with proximal dorsal muscles rather than of an M-mode uniting all the ventral muscles. The M-modes found in this study resemble those reported by Torres-Oviedo and Ting (2007) in their study of the short-latency responses to an unexpected support-surface translation. These authors refer to such muscle groups as “synergies”.

Consider possible kinematical consequences of muscle activation corresponding to the M-modes. Figure 12A illustrates plausible consequences in the body configuration following steady-state activation of muscles corresponding to M_1 and to M_2 together with M_3 . Note that in our study, the time profiles of M_2 and M_3 were similar to each other and differed substantially from the time profile of M_1 . Figure 12B shows kinematic consequences of activating “push-forward” and “push-back” M-modes observed in previous studies involving large COP displacements (Krishnamoorthy et al. 2003a,b). The resulting body configurations in these two panels look similar to those resulting from the eigenmovements proposed by Alexandrov and his colleagues (2001), based on decomposition of the equation of motion of a three-link inverted pendulum in two dimensions. In particular, the kinematics induced by activation of M_1 or M_2+M_3 (see Figure 12A) is similar to the hip eigenmovement (H-eigenmovement) reported

by Alexandrov et al. (2001), i.e. hip flexion combined with ankle plantarflexion (cf. “hip strategy”, Horak and Nashner 1986). On the other hand, activation of the dorsal or frontal groups of muscles (“push-back” and “push-forward” modes, see Figure 12B) leads to consequences similar to the ankle eigenmovements (A-eigenmovement), i.e., rotation of the whole body around the ankle joint (cf. “ankle strategy”, Horak and Nashner 1986).

Alexandrov et al. (2001) showed that, during the same translation of the center of mass (COM; 1 cm in 500 ms), the A-eigenmovement was associated with an almost four times larger COP excursion than the H-eigenmovement (6.5 cm as compared to 1.7 cm). On the other hand, due to the difference in the inertial properties of the body segments (see Alexandrov et al., 2001), the A-eigenmovement is more efficient for slow motions, while the H-eigenmovement is more efficient for fast COM motions (see also Horak and Nashner, 1986; Runge et al., 1999).

The observations of different sets of M-modes in different studies could be related to the different properties of the A- and H-eigenmovements. Namely, the “push-back” and “push-forward” M-modes, likely related to the A-eigenmovement, were found in studies involving large COP shift and relatively small COM motion such as during whole-body sway (Danna-Dos-Santos et al. 2007), preparation to stepping (Wang et al. 2005, 2006), and anticipatory postural adjustments prior to self-induced perturbations (Krishnamoorthy et al. 2003b). In contrast, M-modes likely related to the H-eigenmovement were found in studies involving fast and large COM displacements such as during balance recovery following an external perturbation (Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2007) and large COM acceleration accompanied by a relatively small COP shift (as in the current study).

The results of the current study support the idea that the CNS organizes muscles into a small number of groups (M-modes), within which levels of muscle activation co-vary over a range of similar tasks. Combined with previous reports, they also indicate that M-mode composition can vary in a task-specific way. Note that another group of M-modes, co-contraction modes, have been reported in studies of whole-body tasks performed in unusual conditions (Krishnamoorthy et al. 2004); with practice, these M-modes tend to be replaced with “push-back” and “push-forward” modes (Asaka et al. 2007).

One can only speculate about possible neurophysiological mechanisms involved in the formation of M-modes and M-mode synergies. An attractive metaphor of a *cortical piano* has been suggested by Marc Schieber (Schieber 2001; Schieber and Rivlis 2007). This idea implies that individual cortical neurons (or groups of cortical neurons) are similar to piano keys, while functional movements involve “playing chords”. In other words, neurons that are separated anatomically may be united functionally in groups (*chords*) that produce desired motor effects. Whether such *chords* define M-modes or M-mode synergies is currently unknown.

Hierarchical control of posture and the reference configuration hypothesis

In a large number of studies, indices of muscle activation have been analyzed to get insights into the control of multi-muscle postural tasks (Ivanenko et al. 2004, 2005; Ting and Macpherson 2004; Krishnamoorthy et al. 2003b). Muscle activation patterns may be viewed, in a simplified way, as reflecting two factors, descending signals to the segmental apparatus and reflex feedback from peripheral receptors. The latter factor depends on both descending signals that set the thresholds of activation and the external conditions of movement execution that are typically not perfectly predictable. Hence, the equilibrium-point hypothesis of motor control (Feldman 1966, 1986) assumes that the central controller sets thresholds of muscle activation, while actual levels of activation emerge based on the action of other inputs into the alpha-motoneuronal pools including the tonic stretch reflex.

Recently, the equilibrium-point hypothesis has been generalized to multi-muscle, multi-effector actions. This development, termed the reference configuration hypothesis (Feldman and Levin 1995; Feldman et al. 2007; Pilon et al. 2007), assumes that, at any level of analysis of the neuromotor system, an input from a hierarchically higher level defines a reference configuration, to which the lower level is attracted. In other words, a particular reference configuration constrains all neural and muscular elements to work in a selected spatial frame of reference. If external conditions allow reaching the reference configuration, activity of the elements becomes minimal in accordance with the principle of minimal interaction (Gelfand and Tsetlin 1966). More commonly, however, external constraints, for example those related to the body anatomy and external force fields, prevent the elements from reaching a minimal activation state resulting in a particular muscle activation pattern. A reference configuration defined at a high level of a control hierarchy leads to reference configurations at lower levels of the hierarchy that become emergent properties of the system. Multi-muscle synergies may also be viewed as emergent properties within this scheme.

Within our experiments and analysis, action at the upper level of control may be viewed as specification of a reference configuration in the M-mode space, while composition of the M-modes may be considered using the notion of reference body configurations. Indeed, it is reasonable to expect that, when a controller faces a challenging postural task, it tries to unite muscles into groups such that each group produces a change in the reference body configuration that does not endanger the postural equilibrium. Figure 12A illustrates possible kinematic effects of changes in muscle activation patterns corresponding to modes M_1 and M_2+M_3 . The solid lines show new reference configurations that the body tries to reach. Note that both reference configurations correspond to a change in the body posture that is compatible with only a minor change in the location of the COM in the anterior-posterior direction. In other words, both reference configurations are compatible with vertical posture.

In earlier studies, patterns of changes in the muscle activation patterns corresponding to the most reproducible M-modes involved combined activation of all the ventral muscles (the “push-forward” mode) or combined activation of all the dorsal muscles (the “push-back” mode) (Krishnamoorthy et al. 2003a; Danna-Dos-Santos et al. 2007). These patterns correspond to changes in the reference body configuration illustrated in Figure 12B. Note that the new reference configurations are associated with substantial changes in the COM location. As such, M-modes within this set always have to co-vary to avoid losing balance, while the controller is free to vary at least some of the M-modes in the current study independently.

There seems to be a trade-off between mechanical efficacy and safety (invoked in earlier studies of movements in atypical persons, Latash and Anson 1996, 2006). When the controller performs relatively common tasks such as stepping, quick arm motion, or load manipulation, it organizes muscles into M-modes that are most effective in producing the required mechanical effects. In contrast, when the task is novel (as in the current study), the controller organizes muscles into M-modes corresponding to shifts in the reference body configuration that are safe, although may be not mechanically optimal.

Note that a different “atypical” set of M-modes has been reported in studies when the subjects performed relatively natural tasks while standing on a board with a decreased support area (Krishnamoorthy et al. 2004b; Asaka et al. 2007). Those M-modes involved muscle co-contraction that could be interpreted as a change in the range of joint angle values within which the muscle pairs could be active simultaneously without a change in the body reference configuration. This is another example of using a set of M-modes that, even when recruited individually, are not expected to lead to major COM deviations and loss of balance. In other words, this is another example of trading mechanical efficacy for safety.

Stabilization of two performance variables by the same set of M-modes

The set of three M-modes possesses enough redundancy to ensure stability of two performance variables at the same time. Note that F_X and M_Y time profiles showed relatively strong co-variation during the forward force pulses, but not during the backward pulses (Table 1). Hence, we may assume that stabilization of one of these variables was not necessarily linked to stabilization of the other. Indeed, when indices of multi-M-mode synergies (ΔV) were computed for F_X and M_Y , they showed qualitatively different changes with force pulse direction.

Similar observations have been reported in studies of multi-finger synergies involved in stabilization of the time profiles of the total force and total moment of force (Latash et al. 2001; Scholz et al. 2002; Shim et al. 2004). Those studies have suggested that the control of two performance variables with the same set of effectors may be based on a principle of superposition (Arimoto et al. 2001; Zatsiorsky et al. 2004). According to this principle, separate controllers ensure co-variation within the same set of elemental variables that stabilizes each of the performance variables, and the effects of the two control signals sum up at the level of elemental variables. We observed characteristics of the ΔV index that suggest a similar control principle in postural tasks. On the one hand, both F_X and M_Y could be stabilized simultaneously ($\Delta V > 0$ for both, see Figure 10). On the other hand, ΔV indices for F_X and M_Y showed qualitatively different changes with direction of force pulse. F_X was preferentially stabilized during the backward force pulses, while M_Y showed higher ΔV for the forward force pulses. The differences between the two pulse directions for F_X and M_Y were due to differences in different variance components reflected in ΔV : Higher V_{UCM} for the backward force pulses for F_X and lower V_{ORT} for the forward force pulses for M_Y . The differences between F_X and M_Y observed for the two force pulse directions were also reflected in different changes in the amount of variance accounted for by the linear regression models (see Figure 6).

Although these observations fall short of demonstrating independent control of the two performance variables (F_X and M_Y) using the same set of elemental variables (M-modes), they suggest that this is a likely possibility. Indeed, a possibility of stabilization of two variables and different changes in indexes of synergy with changes in task parameters had been reported in studies of multi-finger synergies (Latash et al. 2001, 2002a) before the principle of superposition received convincing support in more recent studies (Latash and Zatsiorsky 2006; Zhang et al. 2007).

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Figure 1.

A: Schematic representation of the subject's posture during the control trials. The load could act downward (1) or upward (2). B: The subject's posture during the experiments. TA - tibialis anterior, RF - rectus femoris, VM - vastus medialis, RA - rectus abdominis, SOL - soleus, GM - gastrocnemius medialis, GL - gastrocnemius lateralis, BF - biceps femoris, ST - semitendinosus, ES - erector spinae.

Figure 2.

A: The definition of the period of analysis (T_{AN}) for a typical force pulse. The shear force pulse duration (d) was defined between t_{beg} , determined using the second derivative of the shear force time profile, and t_{end} defined by the change of sign of the shear force. The period of analysis (T_{AN}) included the pulse duration and an additional period of $2/3$ of the pulse duration before t_0 . B: An illustration of different time lags between the mechanical variables and the integrated muscle activation indices. Note that, as the time lag increases, the number of common 10% time windows decreases.

Figure 3.

An example of the performances by a typical subject (S3) averaged across 20 pulses (± 1 SD) for the highest target (120 N). A: Forward force pulse. B: Backward force pulse. Panels C and D show data for the forward and backward force pulses, respectively, averaged across all subjects with the standard deviation computed across the subjects. F_X - shear force, M_Y - transversal torque.

Figure 4.

Typical time profiles of EMG signals (rectified and filtered), F_X - shear force, and M_Y - transversal torque averaged across trials for a representative subject (S2), the highest target (120 N) and two directions of shear force production. A: Forward force pulse. B: Backward force pulse. EMG signals of the ventral muscles (TA, RF, VM, and RA) are inverted for better visualization.

Figure 5.

Z-scores of the cosines computed between M-mode vectors M_j and subjects specific central vectors $C_j(s)$, averaged across subjects and force pulse directions (± 1 SD). Note the high z-scores when $i = j$ but not when $i \neq j$.

Figure 6.

Example of changes in the M-mode magnitudes between consecutive time windows computed for the medium target and two directions of shear force pulse: A: Forward force pulse. B: Backward force pulse. The data were averaged across pulses and subjects. Note the similar evolution for M₂ and M₃ as compared to M₁. Error bars show standard errors.

Figure 7.

Percentage of variance explained by the linear regression model between the changes in M-mode magnitudes and the associate changes in F_X - shear force and M_Y - transversal torque. Data are averaged across subjects, target levels, and the two directions of pulse (* - $p < 0.05$). Note the opposite effects of the direction of pulse for the two mechanical variable. Error bars show standard errors.

Figure 8.

The total amount of variance in the M-mode space per degree of freedom (V_{TOT}) is shown for the two directions of shear force production and seven time windows. The data were averaged across targets and subjects. The dashed vertical line shows the force pulse initiation. Note the higher variance during the pulse and higher V_{TOT} for the backward pulses than for the forward pulses. Error bars show standard errors.

Figure 9.

The two components of variance V_{UCM} (variance that lies within the UCM) and V_{ORT} (variance within the orthogonal space) per degree of freedom are shown for the two directions of shear force production, seven time windows, and both mechanical variables (F_X - shear force, M_Y - transversal torque). V_{UCM} (variance that lies within the UCM) and V_{ORT} (variance within the orthogonal space) The data were averaged across targets and subjects. The dashed vertical lines shows the force pulse initiation. Note that for F_X , V_{UCM} was higher for the backward pulses than forward pulses, while V_{ORT} was almost the same for both directions. For M_Y , V_{UCM} was almost the same for the two pulse directions, while V_{ORT} was higher for the backward pulses. Error bars show standard errors.

Figure 10.

Indices ΔV between successive time windows averaged across subjects. Data for the two performance variables - the shear force F_X and the transversal torque M_Y - are presented for the two force pulse directions and the three targets (Low -60 N, Medium - 90 N and High - 120 N). The dashed vertical lines shows the force pulse initiation. Note the differences between the backward and forward pulses. Note also the drop in ΔV during the pulse (after time windows #3) for M_Y and the backward pulses. Error bars show standard errors.

Figure 11.

A: ΔV for both directions of the shear force pulse and the two performance variables (F_X - shear force, M_Y - transversal torque). Data were averaged across subjects, target levels and time intervals. The stars show significant differences from zero ($p < 0.0125$). B: For each time window, ΔV data were averaged across subjects, target levels, and performance variables. The dashed vertical line shows the force pulse initiation. Note the opposite influence of the direction of pulse between the two performance variables (panel A). Note also that, on average, ΔV was higher for the backward pulses than for the forward pulses. This difference was seen mainly during the preparation to the pulse and at its very early phase, i.e. before time window #4 (panel B). Error bars show standard errors.

Figure 12.

Schematic representation of possible kinematic consequences of the M-modes found in this study (A) and M-modes reported previously in sway studies (e.g. Danna-Dos-Santos et al., 2007). The grey stick figures represent the initial body configuration; the black arrows represent the effects of muscle contraction, and the black stick figures show the resulting postures. The grey arrows show the expected motion of the body center of mass (COM).

Table 1
Results of cross-correlation analysis

		R^2_{0lag}	$R^2_{max}(lag \text{ in } \% \text{ of analysis time})$
Forward	Low	0.09	0.61 (12)
	Medium	0.01	0.50 (14)
	High	0.01	0.36 (16)
Backward	Low	0.96	0.97 (-1)
	Medium	0.95	0.96 (-1)
	High	0.91	0.94 (-2)

Averaged across subjects values of R^2 at zero time lag - R^2_{0lag} - and peak R^2 - R^2_{max} - computed between F_X and M_Y time profiles. The data are presented for the two directions of force pulse (forward and backward) and three targets (low, medium, and high). Note the strong influence of the direction of shear force pulse.

Table 2

Results of the PCA Analysis

	Forward			Backward		
	PC ₁	PC ₂	PC ₃	PC ₁	PC ₂	PC ₃
TA	0.38 ± 0.26	0.26 ± 0.39	0.12 ± 0.28	0.42 ± 0.41	0.22 ± 0.41	-0.03 ± 0.27
RF	-0.06 ± 0.07	0.91 ± 0.02	0.09 ± 0.10	0.15 ± 0.36	0.74 ± 0.33	0.12 ± 0.17
VM	0.11 ± 0.17	0.87 ± 0.07	0.11 ± 0.09	0.45 ± 0.38	0.61 ± 0.31	0.08 ± 0.15
RA	-0.08 ± 0.07	0.78 ± 0.14	0.26 ± 0.14	-0.15 ± 0.30	0.45 ± 0.40	0.32 ± 0.27
SOL	-0.21 ± 0.22	0.32 ± 0.17	0.68 ± 0.15	0.08 ± 0.22	0.14 ± 0.22	0.74 ± 0.11
GM	0.18 ± 0.22	0.04 ± 0.11	0.82 ± 0.06	0.13 ± 0.32	-0.07 ± 0.19	0.69 ± 0.21
GL	0.10 ± 0.09	0.23 ± 0.22	0.83 ± 0.08	0.06 ± 0.18	0.06 ± 0.22	0.82 ± 0.09
BF	0.89 ± 0.06	0.09 ± 0.16	0.12 ± 0.14	0.77 ± 0.25	0.17 ± 0.40	0.01 ± 0.15
ST	0.90 ± 0.04	0.01 ± 0.06	0.18 ± 0.17	0.88 ± 0.08	0.11 ± 0.15	-0.03 ± 0.10
ES	0.84 ± 0.05	-0.14 ± 0.07	-0.09 ± 0.11	0.75 ± 0.32	0.06 ± 0.26	-0.10 ± 0.14

Loadings coefficients averaged across subjects (± standard deviation) are shown for each muscle and the two directions of force pulse production. The highest loadings for each muscle are shown in bold. TA - tibialis anterior, RF - rectus femoris, VM - vastus medialis, RA - rectus abdominis, SOL - soleus, GM - gastrocnemius medialis, GL - gastrocnemius lateralis, BF - biceps femoris, ST - semitendinosus, ES - erector spinae.

Table 3

Occurrence of Significant Muscle Loadings

	Forward			Backward		
	PC ₁	PC ₂	PC ₃	PC ₁	PC ₂	PC ₃
TA	3	2	1	4	2	0
RF	0	8	0	1	7	0
VM	0	8	0	4	6	0
RA	0	7	1	1	5	2
SOL	0	2	7	0	1	8
GM	0	0	8	2	0	7
GL	0	1	8	0	0	8
BF	8	0	0	6	2	0
ST	8	0	0	8	0	0
ES	8	0	0	7	1	0

Number of times each muscle was significantly loaded on a PC (loading coefficient > 0.5) is shown for each muscle and the two directions of force pulse production. The highest occurrences are shown in bold. See Table 2 for the abbreviations.