Published in final edited form as:

J Neurophysiol. 2008 February ; 99(2): 500–513. doi:10.1152/jn.01029.2007.

What Do Synergies Do? Effects of Secondary Constraints on Multidigit Synergies in Accurate Force-Production Tasks

Wei Zhang¹, John P. Scholz², Vladimir M. Zatsiorsky¹, and Mark L. Latash¹

¹Department of Kinesiology, Pennsylvania State University, University Park, Pennsylvania

²Department of Physical Therapy and Biomechanics and Movement Science Program, University of Delaware, Newark, Delaware

Abstract

We used the framework of the uncontrolled manifold (UCM) hypothesis to explore changes in the structure of variability in multifinger force-production tasks when a secondary task was introduced. Healthy young subjects produced several levels of the total force by pressing with the four fingers of the hand on force sensors. The frame with the sensors rested on the table (*Stable* condition) or on a narrow supporting beam (*Unstable* conditions) that could be placed between different finger pairs. Most variance in the finger mode space was compatible with a fixed value of the total force across all conditions, whereas the patterns of sharing of the total force among the fingers were condition dependent. Moment of force was stabilized only in the *Unstable* conditions. The finger mode data were projected onto the UCM computed for the total force and subjected to principal component (PC) analysis. Two PCs accounted for >90% of the variance. The directions of the PC vectors varied across subjects in the *Stable* condition, whereas two “default” PCs were observed under the *Unstable* conditions. These observations show that different persons coordinate their fingers differently in force-production tasks. They converge on similar solutions when an additional constraint is introduced. The use of variable solutions allows avoiding a loss in accuracy of performance when the same elements get involved in another task. Our results suggest a mechanism underlying the principle of superposition suggested in a variety of human and robotic studies.

INTRODUCTION

Most human actions are performed with effector systems that have more degrees of freedom than necessary to accomplish the task. Such systems have been addressed as redundant (Bernstein 1967). The problem of controlling redundant systems has been addressed using the notion of *synergies*, defined as neural organizations that ensure high stability (low variability) of important performance variables by coordinating covariation in the space of elemental variables (reviewed in Latash et al. 2002a, 2007). Synergies have been investigated recently within the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999). The UCM hypothesis assumes that the controller organizes two subspaces in the space of elemental variables. One of these spaces (the UCM) corresponds to a fixed value of a potentially important performance variable, and the controller allows relatively large variability of the elemental variables in that subspace. The complementary (orthogonal) subspace corresponds to changes in that performance variable, and the controller tries to limit variability in that subspace.

A number of studies used the framework of the UCM hypothesis to quantify synergies in a variety of tasks and populations (reviewed in Latash and Anson 2006; Latash et al. 2007). Typical analysis in those studies involved the quantitative estimation of two components of variability in the space of elemental variables: “good variability” (V_{UCM} , within the UCM) and “bad variability” (V_{ORT} , orthogonal to the UCM). Synergies have been expected to maximize the proportion of “good” variability in the total variance by promoting covariation among elemental variables that keeps an important performance variable at a desired value (reduces its trial-to-trial variability). Thus synergies have been quantified by comparing the relative amounts of “good” and “bad” variance within the space of elemental variables. However, little attention has been paid to possible structure of variability within each of the two subspaces, particularly within the UCM. This is, however, an important issue that has direct relevance to the question: What is the purpose of motor synergies?

Synergies have been viewed as a means of decreasing variability in important performance variables. This view has been reflected not only in terms like “error compensation” and “compensated variability” (Latash et al. 1998; Scholz et al. 2002) but also in models based on the action of feedback loops (Latash et al. 2005; Todorov and Jordan 2002). Another attitude to synergies, however, is that their main purpose is to allow the controller to perform several tasks simultaneously, for example to open a door handle by pressing on it with the elbow while carrying a cup of coffee in the hand.

A number of studies documented simultaneous stabilization of the total force and total moment of force in multidigit pressing (Latash et al. 2001, 2002b; Scholz et al. 2002; Zhang et al. 2006, 2007) and prehension (reviewed in Latash et al. 2004; Zatsiorsky et al. 2003) tasks. These studies have suggested that the control of the human hand is based on the principle of superposition introduced earlier in robotics for the control of grippers (Arimoto et al. 2001; Doulgeri et al. 2002; Parra-Vega et al. 2001). This principle suggests that a skilled action can be decomposed into several elemental subactions that are controlled independently by separate controllers. In robotics, such a decoupled control decreases the computation time.

Several kinematic variables have been shown to be stabilized by covaried changes in joint angles during sit-to-stand action (Scholz et al. 2001), quick-draw pistol shooting (Scholz et al. 2000), voluntary body sway (Freitas et al. 2005), and spontaneous postural sway (Hsu et al. 2007). Several studies documented a counterintuitive drop in “good variability” with practice (Domkin et al. 2002, 2005; Latash et al. 2003); these observations have been interpreted as reflecting possible stabilization of variables other than those related to the explicit task. All these studies suggest that variability within the UCM computed for a performance variable may be structured differently depending on whether the controller also tries to stabilize other performance variables.

This study is the first to explore changes in the structure of variability within the UCM in the presence of two tasks: explicit (primary) and secondary. Since this is an exploratory study, we focused on general questions such as the following. Are there default patterns of covariation among elemental variables within the UCM that are common across subjects in the absence of a secondary task? Will a secondary task lead to weaker synergies stabilizing the performance variable associated with the primary task? Will a secondary task lead to less variable (more reproducible across subjects) solutions in the space of elemental variables, particularly in the UCM subspace? We used multifinger accurate force production as the primary task and manipulated constraints on the moment of force produced by the fingers in a frontal plane as the secondary task.

METHODS

Subjects

Ten healthy volunteers [age: 28.2 ± 0.9 (mean $\pm$ SE) yr], five males and five females, participated as subjects in the experiments. The average mass of the subjects was 63.7 ± 2.9 kg and the average height was 171.8 ± 2.4 cm. All the subjects were right-handed according to their preferred hand use for writing and eating. Their right-hand width (measured at the metacarpophalangeal joint level) averaged 8.2 ± 0.3 cm and the right-hand length (measured from the midpoint of the transverse wrist crease to the tip of the middle finger) was 18 ± 0.4 cm. All subjects gave informed consent according to the procedures approved by the Office for Research Protection of the Pennsylvania State University.

Apparatus

The experimental setup is illustrated in Fig. 1. Four 1.5-cm-diameter unidirectional piezoelectric force sensors (model 208C02; Piezotronic) were used to measure the forces produced by each of the four fingers of the right hand (I, index; M, middle; R, ring; and L, little; Fig. 1B). Each sensor was covered with a cotton pad to increase friction and to prevent the influence of finger skin temperature on the measurements. The sensors were positioned along the four parallel slots (0.06 m long) on a Plexiglas plate (0.15×0.25 m). The sensors were mediolaterally distributed 0.03 m apart. The position of the sensors on the plate could be adjusted in the forward-backward direction along the slots to fit the individual subject's anatomy. There were three grooves (0.12 m long) underneath the Plexiglas plate parallel to the slots and positioned between the slots for the I- and M-finger sensors, for the M- and R-finger sensors, and for the R- and L-finger sensors. An aluminum inverted-T-shape bar (0.11 m long) was fixed onto the top of the table. The vertical end of the inverted-T-shape bar was sharpened to reduce the friction when it was fitted into one of the grooves under the Plexiglas plate to act as a pivot during *Unstable* condition tests (subsequently introduced). The width of the pivot was 0.5 mm. There were two more slots on the two sides of the plate that were used to mount counterloads to balance the setup in *Unstable* conditions when the pivot was between the I and M fingers and between the R and L fingers. Figure 1C shows the front view of the plate with the sensors resting on the pivot. The counterload (132 g) was used to ensure that the plate with the sensors and the load was balanced with respect to the pivot in the absence of finger forces. The total weight of the plate with the sensors and the counterload was 4.8 N.

Analog output signals from the sensors were processed by separate AC/DC conditioners (M482M66; Piezotronic) with the $\pm 1\%$ error range over the typical epoch of recording of a constant signal. The force measured by each sensor was sampled at 1,000 Hz, with the 32-bit resolution by a desktop computer. The sensors were calibrated 30 min before each testing.

During testing, the subject sat comfortably in a chair facing the testing device with his/her right upper arm at about 45° of abduction in the frontal plane and 45° of flexion in the sagittal plane, the elbow at about 45° of flexion (full extension corresponds to 0°). A wooden horizontal board supported the wrist and the forearm; two pairs of Velcro straps were used to prevent forearm motion during the tests. A custom-fitted wooden piece was placed underneath the subject's right palm and attached on the supporting wooden board to help maintain a constant position and configuration of the hand and fingers. One more pair of Velcro straps ensured that the wooden piece was stable with respect to the board. A 17-in. liquid crystal display monitor, placed about 65 cm in front of the subject, displayed both the task (target total force time profile) and the actual total normal force produced by the four fingers.

Procedure

Subjects were instructed to complete two auxiliary force-production tasks (*MVC* and *Ramp*) and one main experimental task (*Steady-state*) (Fig. 1A). All trials started with the subject sitting quietly and placing the fingers of the right hand on the force sensors. The subject was instructed to be relaxed and to rest the weight of the hand and fingers on the sensors. Sensor signals were put to zero at that moment such that only deviations from the resting conditions were recorded and analyzed. Then, a sound signal generated by the computer informed the subject to get ready for a new trial. Then a trace showing the total force produced by the explicitly instructed finger(s) (master fingers) started to move across the screen.

The first auxiliary force-production task required the subjects to produce maximal pressing force [maximal voluntary contraction (MVC)] by all four fingers (MVC_{IMRL}) together (Fig. 1A, *left*). The subjects were instructed to produce peak force within a 2-s time window shown on the screen and then to relax. Two trials were performed in the *MVC* task for each subject with 30-s intervals between the trials, and the data for the trial with a higher peak force were used for setting up further tasks.

The second auxiliary force-production task (*Ramp*) required the subject to follow a dashed template line shown on the screen with the cursor representing the force produced by an instructed finger (I, M, R, or L). The template line was a combination of straight-line segments: a horizontal segment corresponded to zero force for the first 2 s, followed by an oblique line going up to 10% of the participant's individual MVC_{IMRL} over 4 s, followed by another horizontal line corresponding to this constant force level for ≥ 2 s (Fig. 1A, *center*). Subjects performed one *Ramp* trial with each finger. The subjects were instructed to pay no attention to possible force generation by other, explicitly noninvolved fingers, as long as the master finger produced the required force. The subjects were not allowed to lift fingers off the sensors at any time. The *Ramp* tests were used to calculate the enslaving matrix used in the uncontrolled manifold analysis (subsequently described).

The main task (*Steady-state*) required the subjects to produce a series of steady-state levels of the total force (F_{TOT}), computed as the sum of individual normal finger forces. The time profile shown on the screen consisted of four horizontal segments, which corresponded to zero force over 1 s, and then 5, 7.5, and 10% of MVC_{IMRL} ; each segment's duration was 3 s (Fig. 1A, *right*). The instruction was to follow as accurately as possible the lines with the cursor showing the total finger force.

During the *Steady-state* tests, four task conditions were introduced by placing the Plexiglas plate with the force sensors directly on the table (*Stable*) or on the inverted-T-shape bar (*Unstable*) (Fig. 1B). In the *Unstable* conditions, the inverted-T-shape bar was fit into one of the grooves underneath the Plexiglas plate between I and M fingers (*Pivot-IM*), M and R fingers (*Pivot-MR*), and R and L fingers (*Pivot-RL*) in different series. Under the *Unstable* conditions, the subjects were also instructed to keep the Plexiglas plate with the sensors horizontal at all times. Crude violations of this instruction were obvious when either end of the plate touched the table. This happened when the plate deviated from the horizontal orientation by 10° for *Pivot-MR* and by 8 and 12° for *Pivot-IM* and *Pivot-RL*. Tests under the *Stable* condition were always performed prior to the *Unstable* conditions to avoid biasing the subjects by exposing them to tests that required balancing the total moment of force produced by the fingers. The *Pivot-IM*, *Pivot-MR*, and *Pivot-RL* conditions were presented in a balanced order across subjects. For all conditions, 24 consecutive trials were collected after 5 practice trials. Trials with lost equilibrium (there were no more than 3 trials per condition for each subject) in *Unstable* conditions were discarded and repeated immediately. Intervals between the trials were 8 s; intervals between the tasks were ≥ 2 min.

Initial data processing

Data processing was performed off-line using MATLAB 7.0, Excel, and Minitab software. In the *MVC* tests, peak forces were measured at the time when the sum of the forces produced by the four fingers (MVC_{IMRL}) reached its peak. For the trials with steady-state force production, average time profiles for finger forces as well as their variability indices, such as SD and variance, were computed across trials for each time sample. For across-subject comparisons, the variance indices for the total force and for the total moment of force were normalized by the individual subject's values of $(MVC_{IMRL})^2$ and $(0.03MVC_{IMRL})^2$, respectively; the lever arm of 0.03 m was selected as typical of the action of fingers. This simplification considers only the contribution of the normal finger forces to the total moment of force in the frontal plane. We have assumed that the subjects followed the instruction of pressing down on the sensors and that the contribution of free moments and moments produced by shear finger forces was small. All the outcome variables, subsequently described in further detail in this section, were averaged for each condition and each subject over 200 ms in the middle of each of the intervals corresponding to different steady-state force levels (5, 7.5, and 10% of MVC_{IMRL}).

Finger sharing patterns

Finger sharing was defined as the percentages of F_{TOT} produced by the individual fingers (S_i , $i = I, M, R, L$). S_i indices were computed for each time sample and then averaged over the 200-ms time windows in the middle of the steady-state force intervals. Further, these indices were averaged across the three force levels, since there were no significant differences across the force levels (see RESULTS).

The UCM analysis

The uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999; Schöner and Scholz 2007; reviewed in Latash et al. 2002a, 2007) assumes that the controller organizes covariation among elemental variables to stabilize a certain value of a performance variable [total force (F_{TOT}) and total moment of force (M_{TOT}) in our study]. Finger forces covary across all tasks because of the phenomenon of *enslaving*, i.e., unintended force production by fingers when other fingers of the hand produce force (Kilbreath and Gandevia 1994; Li et al. 1998; Ohtsuki 1981; Zatsiorsky et al. 1998). Thus the first step of the analysis was to convert the data from time series of finger forces to time series of elemental variables, force modes (Danion et al. 2003) that can, at least hypothetically, be changed by the controller one at a time.

Force modes were defined similarly to previous studies (Latash et al. 2001; Scholz et al. 2002). Briefly, single-finger *Ramp* trials were used to compute a (4×4) enslaving matrix $\mathbf{E}$ for each subject. The entries of the $\mathbf{E}$ matrix were computed as the ratios of the change in the force of a finger to the change in the total force over the ramp duration. The four columns of the $\mathbf{E}$ matrix correspond to *Ramp* trials performed by the four fingers. The $\mathbf{E}$ matrix was used to compute changes in the vector of hypothetical commands to fingers (force modes, $\mathbf{m}$) based on force changes, according to

$$\mathbf{m}_{ij} = \mathbf{E}^{-1} \times \mathbf{f}_{ij} \quad (1)$$

where $\mathbf{i}$ stands for the time samples and $\mathbf{j}$ stands for the trials.

Further analysis was done across the 24 trials performed by a subject in a given condition for each time sample over the duration of the task. For each time $\mathbf{t}_i$ the average vector of force modes $\mathbf{m}_{AV}$ was computed. Then, for each trial $\mathbf{j}$, the deviation ($\Delta\mathbf{m}_j$) between $\mathbf{m}_j$ and $\mathbf{m}_{AV}$ was computed. In the four-dimensional $\Delta\mathbf{m}$ space, subspaces were computed corresponding to the average value of F_{TOT} (V_{UCM-F}) and to the average value of M_{TOT} (V_{UCM-M}). These

subspaces corresponded to changes in $\Delta \mathbf{m}$ that kept the corresponding performance variable, F_{TOT} or M_{TOT} , unchanged. Variance of the $\Delta \mathbf{m}_j$ data set was then computed along a direction orthogonal to V_{UCM-F} and orthogonal to V_{UCM-M} . We will refer to these indices as V_{ORT-F} and V_{ORT-M} , respectively. This was done using the Raleigh fraction, which can be used to compute variance of a set of data points (vectors) in a multidimensional space after projecting them onto an arbitrary vector in that space. The length of a projection of vector $\mathbf{x}$ on vector $\mathbf{v}$ is $\mathbf{v}^T \mathbf{x} / (\mathbf{v}^T \mathbf{v})^{0.5}$; its squared value can be written as $\mathbf{v}^T \mathbf{x} \mathbf{x}^T \mathbf{v} / \mathbf{v}^T \mathbf{v}$. For a demeaned set of K vectors $\{\mathbf{x}_i\}$, the variance in the direction of $\mathbf{v}$ is $\mathbf{v}^T \sum_{i=1}^K \mathbf{x}_i \mathbf{x}_i^T \mathbf{v} / (K-1) \mathbf{v}^T \mathbf{v}$. This formula can be rewritten as $\mathbf{v}^T \text{cov}(\mathbf{x}) \mathbf{v} / \mathbf{v}^T \mathbf{v}$, which is the Rayleigh fraction with vector $\mathbf{v}$ and covariance matrix of the vector set $\{\mathbf{x}_i\}$. Two vectors $\mathbf{v}$ were selected, orthogonal to V_{UCM-F} and orthogonal to V_{UCM-M}

$$V_{ORT} = \frac{\mathbf{J}_m \text{cov}(\mathbf{m}) \mathbf{J}_m^T}{\mathbf{J}_m \mathbf{J}_m^T} = \frac{\mathbf{J} \mathbf{E}^{-1T} \mathbf{E}^{-1} \text{cov}(\mathbf{f}) \mathbf{E}^{-1T} \mathbf{E}^{-1} \mathbf{J}^T}{\mathbf{J} \mathbf{E}^{-1T} \mathbf{E}^{-1} \mathbf{J}^T} \quad (2)$$

where $\mathbf{J}$ is a Jacobian matrix relating small changes in modes ($\mathbf{J}_m$) or forces ($\mathbf{J}$) to changes in the selected performance variable (F_{TOT} or M_{TOT}); total force in this study, $\text{cov}(\mathbf{m})$, is the covariance matrix in the mode space for the demeaned sets of vector $\mathbf{m}$; $\text{cov}(\mathbf{f})$ is the covariance matrix in the finger force space for the demeaned sets of vector $\mathbf{f}$; $\mathbf{E}^{-1}$ stands for the inverse of $\mathbf{E}$; and T is the sign of transpose. For the hypothesis that F_{TOT} was stabilized by covaried changes in the finger modes across trials (the force-stabilization hypothesis), $\mathbf{J} = [1, 1, 1, 1]$. For the hypothesis that M_{TOT} was stabilized by covaried changes in the finger modes across trials (moment-stabilization hypothesis), $\mathbf{J} = [d_I, d_M, d_R, d_L]$, where d represents the lever arms of individual fingers; d values were negative for finger modes that contributed to supination efforts. Note that $\mathbf{J}$ values are written as vector-rows. $\mathbf{J}_m$ can be computed as: $\mathbf{J}_m = \mathbf{J} \mathbf{E}^{-1T}$, where $\mathbf{E}^{-1T}$ is the transpose of $\mathbf{E}$ inverse.

V_{ORT} reflects the amount of mode variance in the data set that corresponds to a change in the selected performance variable. The difference between the total amount of variance (V_{TOT}) and V_{ORT} corresponds to variance that does not affect the average value of the performance variable. We will address this variance as V_{UCM} (variance within the uncontrolled manifold): $V_{UCM} = V_{TOT} - V_{ORT}$. Note that the finger mode space is four-dimensional; V_{ORT} lies along a one-dimensional subspace, whereas V_{UCM} lies in a three-dimensional subspace. Therefore to compare the amounts of variance per dimension, the following index was used

$$\Delta V = \frac{(V_{UCM}/3) - (V_{ORT}/1)}{V_{TOT}/4} \quad (3)$$

Normalization by the total amount of variance per dimension ($V_{TOT}/4$) was used to compare the data across subjects who could show different amounts of the total variance. Note that positive values of ΔV correspond to proportionally higher V_{UCM} than V_{ORT} . Thus values $\Delta V > 0$ may be interpreted as a reflection of a multimode synergy stabilizing that performance variable. If $\Delta V = 0$, the amount of variance per dimension is the same in directions that correspond to a change in the selected performance variable and those along directions that keep the variable unchanged; $\Delta V < 0$ may be interpreted as covariation among changes in finger modes contributing to a change in the selected performance variable or destabilizing it (cf. Bienaymé equality theorem; Loeve 1977).

ΔV indices were computed for F_{TOT} (force-stabilization hypothesis, ΔV_F) and M_{TOT} (moment-stabilization hypothesis, ΔV_M) separately for each subject and each condition. Further, these

indices were averaged over the middle 200 ms within each steady-state force interval and then compared across subjects and conditions.

PCA analysis

Variance within UCM_F —by definition—does not affect F_{TOT} . Thus to examine how imposing the secondary task of M_{TOT} stabilization affected force-mode control related to F_{TOT} stabilization (as compared with the *Steady-state* task), the vector of finger force modes of each trial within a condition was projected onto the UCM for F_{TOT} for each time sample of that data set. Principal component analysis (PCA) was then applied to the vector projections across trials to determine whether relations among finger modes within the UCM for stabilizing total force depended on M_{TOT} constraints. This analysis involved the following steps.

STEP 1: PROJECTION MATRIX CALCULATION—To project the $\Delta \mathbf{m}$ data onto UCM_F , a projection matrix ($\mathbf{P}$) was computed so that the projections of modes into the UCM were represented in the coordinates of the original mode space rather than in the coordinates of the UCM subspace. UCM_F subspace can be represented as the null space of the Jacobian matrix of finger modes

$$N_j = \text{Null}(\mathbf{J}_m) = [e_1 \quad e_2 \quad e_3] = \begin{bmatrix} e_1^i & e_2^i & e_3^i \\ e_1^m & e_2^m & e_3^m \\ e_1^r & e_2^r & e_3^r \\ e_1^i & e_2^i & e_3^i \end{bmatrix} \quad (4)$$

where e_i^k represents the coordinate of the i th basis vector of the null space of the Jacobian matrix on the k coordinate axis of the finger mode space.

Assume $\mathbf{v}$ is an original matrix that has to be projected. The projected matrix $\mathbf{v}_p$ can be calculated by cross-multiplying $\mathbf{P}$ and $\mathbf{v}$ or by cross-multiplying basis vectors of UCM subspace ($\mathbf{e}$) and coordinates of $\mathbf{v}$ in the UCM subspace

$$\begin{aligned} \mathbf{v}_p &= \mathbf{P} \times \mathbf{v} \\ &= \vec{e} \times k_1 \vec{e}_1 + k_2 \vec{e}_2 + k_3 \vec{e}_3 \\ &= \vec{e} \times (\vec{e}^T \times \mathbf{v}) = \vec{e} \times \vec{e}^T \times \mathbf{v} \end{aligned} \quad (5)$$

Consequently, the projection matrix $\mathbf{P}$ to project force modes onto the null-space of $\mathbf{J}$ was calculated as

$$\mathbf{P} = \vec{e} \times \vec{e}^T = N_j \times (N_j^T \times N_j)^{-1} \times N_j^T \quad (6)$$

where $\mathbf{P}$ is normalized by $(N_j^T \times N_j)^{-1}$.

STEP 2: MODE CORRECTION FOR THE LEVER ARMS—When a finger modified its force during a steady-state trial, other fingers were also expected to change their forces because of the enslaving. Thus a mode change for a finger led to a resultant force change that was applied not in the middle of that finger's force sensor, but at a different point (R_m) where the resultant force acted given the enslaving effects. The lever arm of such a resultant force also depended on the location of the pivot, different in different conditions. Since we have been interested in the effects of moment constraints on finger mode interaction, prior to further PCA

procedures, we introduced a correction transformation for force modes to make variations in each mode equivalent in their effects on the total moment of force with respect to the pivot. Each individual force mode was multiplied by its lever arm (L_k , $k = I, M, R, L$) computed with respect to pivot position ($L_{PIV} = 0$). This procedure resulted in a set of corrected mode vectors, $\mathbf{m}_C$

$$\mathbf{m}_C = \mathbf{m}_{ijk} \times L_k \quad (7)$$

where i refers to a time sample, j refers to a trial, and k refers to a finger.

The lever arm (L_k) in Eq. 7 was calculated as the shortest distance between the point of application (R_m) of each mode's resultant and L_{PIV}

$$L = R_m - L_{PIV} \quad (8)$$

In Eq. 8, L was considered positive when the pivot was to the right of R_m . To compute R_m , we considered the center of the I-finger sensor as the origin of coordinate. Since the entries of the enslaving matrix $\mathbf{E}$ have been assumed constant over a range of efforts (see Li et al. 1998; Zatsiorsky et al. 1998), the individual finger forces were involved proportionally over a range of mode values for each of the four modes. This allows one to introduce a notion of mode application point, which is, by definition, the coordinate of application of the resultant force. This coordinate was computed as the point with respect to which the total moment of force produced by the four fingers was zero, assuming only one mode involvement at a time.

STEP 3: MODE PROJECTION ONTO UCM_F—Corrected modes, $\mathbf{m}_C$, were projected onto UCM_F ($\mathbf{P}_{UCM_F}$) with the help of a projection matrix $\mathbf{P}$ (projection matrix of the Jacobian in modes) with $\mathbf{m}_C$

$$\mathbf{P}_{UCM_F} = \mathbf{m}_C \times \mathbf{P} \quad (9)$$

Before running PCA, the data were processed as follows. Each individual finger force was averaged over each of the 8 consecutive 25-ms windows within the 200-ms interval selected in the middle of each steady-state force level (see earlier text). Consequently, we had 192 samples = 8 windows $\times$ 24 trials for each force level and for each subject. PCA analysis was performed by using Matlab based on the correlation matrix (4 modes $\times$ 192 samples) of $\mathbf{P}_{UCM_F}$. The UCM_F space is three-dimensional. Thus although the M-mode space is four-dimensional, the PCA resulted in three PCs accounting for 100% of the variance. Varimax rotation with factor extraction (two factors) was performed. The two resulting PCs and corresponding variances are subsequently presented in RESULTS. The third PC typically accounted for <10% of the variance.

Statistical analysis

Standard methods of parametric statistics were used; data are presented as means and SEs. ANOVA with repeated measures was used to analyze indices of variance, sharing, and synergies with factors: *Condition* (four levels: *Stable*, *Pivot-IM*, *Pivot-MR*, and *Pivot-RL*) and *Force Level* (three levels: 5%, 7.5%, and 10% of MVC). A factor ΔV -Index (two levels: ΔV_F and ΔV_M) was used for ANOVAs on indices of synergy, ΔV_F and ΔV_M . Data expressed in percent (sharing of finger force, variance explained by principal components) were subjected to z-transformation before using parametric methods of analysis. Tukey's honestly significant difference tests and pairwise contrasts were applied to further explore significant effects.

RESULTS

Performance of the main task

The average maximal F_{TOT} in the MVC tests across subjects was 88.0 ± 9.2 N. The average target values of the total force set for the *Steady-state* task thus were 4.4, 6.6, and 8.8 N. These values differed across subjects since they were computed based on individual MVC_{IMRL} values.

Figures 2 and 3 show the typical time profiles of F_{TOT} and M_{TOT} , respectively, during the four conditions in the *Steady-state* task produced by a typical subject. Each panel shows 24 time profiles recorded in consecutive trials. For the *Stable* condition, M_{TOT} was computed with respect to the midpoint between the M and R fingers. Figure 2 shows that the subject produced consistent F_{TOT} profiles across trials and kept a steady-state F_{TOT} value at most times, except the transition periods. Figure 3 shows that M_{TOT} was more variable and its variability increased for larger force levels. Note the large variability of M_{TOT} under the *Stable* condition (Fig. 3, top left).

Variance of F_{TOT} (V_F) and M_{TOT} (V_M) was computed across trials for each condition and each subject. Further, these indices were averaged over 200-ms time windows in the middle of each of the steady-state force intervals. For across-subject comparison, these indices were further normalized by the individual subject's MVC_{IMRL} squared. Figure 4 shows the averaged across-subject normalized indices ($V_{F,N}$ in Fig. 4A and $V_{M,N}$ in Fig. 4B). Force variance was the lowest for the *Stable* condition, and it did not show a clear trend with an increase in the target force level. In contrast, moment variance was the highest for the *Stable* condition, and it showed an increase with an increase in the target force level. When only *Unstable* conditions were considered, force variance tended to be the highest for the *Pivot-RL* condition, whereas moment variance was the lowest for the *Pivot-MR* condition.

These observations have been confirmed by a two-way ANOVA on $V_{F,N}$, *Condition* (*Stable*, *Pivot-IM*, *Pivot-MR*, and *Pivot-RL*) $\times$ *Force Level* (5, 7.5, and 10%). There was only a main effect of *Condition* [$F_{(3,108)} = 3.3$; $P < 0.05$]. Post hoc Tukey's tests indicate that $V_{F,N}$ at the *Pivot-RL* condition was significantly higher than that at the *Stable* condition ($P < 0.05$). A similar two-way ANOVA on $V_{M,N}$, *Condition* $\times$ *Force Level*, showed main effects of *Condition* [$F_{(3,108)} = 17.49$; $P < 0.001$] and of *Force Level* [$F_{(2,108)} = 10.74$; $P < 0.001$] without significant interactions. Post hoc Tukey's tests confirmed higher $V_{M,N}$ in the *Stable* condition compared with all three *Unstable* conditions ($P < 0.001$). Tukey's tests also showed that $V_{M,N}$ at 10% MVC was significantly higher than that at 5% MVC ($P < 0.001$) and at 7.5% MVC ($P < 0.05$).

Finger sharing patterns

Figure 5 shows the average sharing patterns of individual fingers (S_I , S_M , S_R , S_L) under different conditions (A: *Stable*; B: *Pivot-IM*; C: *Pivot-MR*; and D: *Pivot-RL*). Under the *Stable* condition, the forces produced by the I and M fingers accounted for >70% of F_{TOT} . Under the *Pivot-IM* and *Pivot-RL* conditions, about 60% of F_{TOT} was produced by the I and L fingers, respectively. Under the *Pivot-MR* condition, individual fingers shared F_{TOT} most evenly.

S_i values were log-transformed into z-scores and subjected to ANOVAs with factors *Condition* (*Stable*, *Pivot-IM*, *Pivot-MR*, and *Pivot-RL*) and *Force Level* (5, 7.5, and 10%). There was a main effect of *Condition* for all four shares [$F_{(3,108)} > 48.0$; $P < 0.001$]. Post hoc Tukey's tests indicate that 1) S_I was significantly different across all conditions ($P < 0.001$) with the highest values for *Pivot-IM* and the lowest values for *Pivot-RL*; 2) S_M was significantly different across all conditions ($P < 0.005$) with the highest values for *Stable* and the lowest values for *Pivot-RL*; 3) S_R was significantly different across all conditions ($P < 0.001$) except between

Pivot-MR and *Pivot-RL*; it showed the lowest value at *Pivot-IM*; and 4) S_L was significantly different across all conditions ($P < 0.001$) except between *Stable* and *Pivot-IM*; it showed the largest value for the *Pivot-RL* condition.

Uncontrolled manifold (UCM) analysis

The UCM analysis was used to quantify the multifinger synergies in the space of force modes (see METHODS). A normalized index (ΔV) was computed with respect to two performance variables, F_{TOT} and M_{TOT} (ΔV_F or ΔV_M , respectively). Recall that positive values of ΔV indicate synergies stabilizing that particular performance variable. Larger positive values of ΔV correspond to proportionally more variance in the mode space compatible with a stable value of F_{TOT} (or M_{TOT}).

Figure 6 presents the time profiles of ΔV_F (A) and ΔV_M (B) under the four task conditions for a typical subject. Solid lines show the data for the *Stable* condition, whereas dashed lines represent the three *Unstable* conditions. The time axis in Fig. 6 shows three intervals corresponding to the three levels of F_{TOT} marked by the vertical dotted lines and arrows. Note the consistently positive values of ΔV_F over the steady-state F_{TOT} intervals and the transient drops in ΔV_F during the force transition intervals. These results were obtained under all conditions. ΔV_M showed consistently high values under all three *Unstable* conditions, but its values under the *Stable* condition were negative. Note also that ΔV_M showed no transient drops under the *Unstable* conditions when the force level changed. Such patterns were typical of all ten subjects.

Since ΔV indices did not show a dependence on force level, these indices were averaged over the 200-ms time windows in the middle of the steady-state force intervals and then across the force levels. Figure 7 showed ΔV_F (A) and ΔV_M (B) averaged across subjects with SEs. Note the very high average values of ΔV_F approaching 1.2 (note that the theoretically possible highest value corresponding to a perfect synergy is 1.33; $V_{TOT} = V_{UCM}$, $V_{ORT} = 0$ in Eq. 3). Under the *Unstable* conditions, the average values for ΔV_M are more modest, but still significantly positive. These values are not different from zero for the *Stable* condition.

A three-way ANOVA on ΔV indices, *Condition* (*Stable*, *Pivot-IM*, *Pivot-MR*, and *Pivot-RL*) $\times$ *Force Level* (5, 7.5, and 10%) $\times$ ΔV -*Index* (ΔV_F and ΔV_M) confirmed main effects of *Condition* [$F_{(3,230)} = 25.81$; $P < 0.001$] and of *Variable* [$F_{(1,230)} = 181.57$; $P < 0.001$], as well as a significant interaction between *Condition* and *Variable* [$F_{(3,230)} = 28.45$; $P < 0.001$]. Post hoc Tukey's tests confirmed that ΔV_M indices under the *Stable* condition were significantly lower than those under the three *Unstable* conditions ($P < 0.001$). In addition, ΔV_F was significantly higher than ΔV_M ($P < 0.0001$) and this difference was greater under the *Stable* condition ($P < 0.001$).

PCA within the UCM

Recall that principal component analysis (PCA) was applied to data projected onto the UCM_F subspace, computed for each subject and at each time sample, for the average value of total force observed across 24 trials within each condition. Three principal components (PCs) and their percentage values of explained variance ($pc\%$) were computed for each force level under each task condition and for each subject. The amount of variance explained by each PC was similar across the three force levels within each subject and also across subjects. Average values of $pc1\%$, $pc2\%$, and $pc3\%$ were 62.2 ± 1.21 , $28.05 \pm 0.96\%$, and $9.75 \pm 0.88\%$, respectively. The $pc\%$ values were z-transformed for further statistical analysis. Then, a two-way ANOVA was performed on z-scores for $pc3\%$, *Condition* $\times$ *Force Level*. There was a main effect of *Condition* [$F_{(3,108)} = 18.59$; $P < 0.001$]. Post hoc Tukey's tests indicated that $pc3\%$ under the *Pivot-MR* condition was significantly lower than that under the other three

conditions ($P < 0.001$). In addition, $pc3\%$ under the *Pivot-RL* condition was significantly larger than that under the *Stable* condition ($P < 0.01$).

Since $>90\%$ of variance was accounted for by *PC1* and *PC2*, factor rotation with extraction of two PCs was performed, following *Varimax* criteria. This procedure resulted in two new PCs (*PC1'* and *PC2'*). The composition of PCs (loading coefficients) varied substantially across subjects; so, we decided not to average data across subjects but to perform classification of PCs based on the sets of significantly loaded modes (those with the loading factors >0.5).

Table 1 shows the PCA results for a typical subject (subject #2). The loading factors for the four corrected modes ($\mathbf{m}_C$; see METHODS) and $pc\%$ are presented for each of the three force levels (F_1 , F_2 , F_3) under each of the four conditions (*Stable*, *Pivot-IM*, *Pivot-MR*, *Pivot-RL*). The loading factors are shown in the order I, M, R, L (top-down). Significant loading factors (>0.5 in absolute magnitude) are shown in bold.

Over all the conditions, all the PCs could be classified into three groups based on the number of fingers significantly loaded: one-finger PCs, two-finger PCs, and three-finger PCs. Two two-finger PCs showed up most frequently, especially under the *Unstable* conditions. For these most typical PCs, either $\mathbf{m}_C$ for I and M loaded significantly but with opposite signs (I-M) or $\mathbf{m}_C$ for R and L loaded significantly, also with opposite signs (R-L). These most typical PCs had $\mathbf{m}_C$ for I and M significantly loaded but with opposite signs (I-M) and $\mathbf{m}_C$ for R and L significantly loaded, also with opposite signs (R-L). To simplify description, we are going to represent PCs with a vector of loading coefficients using +1 and -1 for the loadings of more than +0.5 and less than -0.5, respectively. We will use 0 for the loadings with the absolute values <0.5 . Under this convention, the typical I-M and R-L PCs can be represented as [1 -1 0 0] and [0 0 1 -1]. Note that the PCA procedure makes [1 -1 0 0] equivalent to [-1 1 0 0].

The total number of PCs was 240, 2 PCs $\times$ 3 force levels $\times$ 4 conditions $\times$ 10 subjects. Table 2 summarizes the frequency of occurrence of all the PC patterns over all subjects. Ten two-finger PC patterns, eight three-finger PC patterns and four one-finger PC patterns were observed across subjects. Across those 22 PC patterns, I-M and R-L were the most common, adding ≤ 110 occurrences, close to 50% of all the PC patterns. Further, we will address these two PC patterns as “default PCs.” The two default PCs were present most frequently under the *Pivot-MR* condition and least frequently under the *Stable* condition. These differences were confirmed by nonparametric, Mann-Whitney tests, showing that these two PCs were more common under the *Pivot-MR* condition than under any of the other three conditions ($P < 0.01$).

Eight three-finger PC patterns were observed. All these three-finger PCs could be viewed as derived from the two “default” two-finger PCs (I-M and R-L), by adding a third finger. Figure 8 describes the three-finger PCs as derivatives from the I-M and R-L PCs. In Fig. 8, shaded fingers represent those significantly loaded, whereas different shades (black and gray) indicate different signs of the loading factors.

Under the *Stable* condition, and with the pivot between the M and R fingers (*Pivot-MR*), the two default PCs (I-M and R-L) can be viewed as stabilizing the total moment of force. In other words, the significantly loaded fingers produce moments of force in opposite directions about the pivot. This is not necessarily true for conditions *Pivot-IM* and *Pivot-RL*. Moment of force stabilization under the *Pivot-IM* condition could benefit from the R-L PC, but it would be hurt by the I-M PC (that is, the I-M PC indicates that increases in F_I are accompanied by decreases in F_M and vice versa. This would tend to increase the moment about the pivot between I and M. In contrast, the R-L PC would minimize force changes on the ulnar side of the I-M pivot (thus stabilizing the moment about the pivot). Under the *Pivot-RL* condition, total moment of force could be stabilized by the I-M PC, but not by the R-L PC. Of all the default PC occurrences under the *Pivot-IM* and *Pivot-RL* conditions, about 50% were apparently contributing to

M_{TOT} stabilization, whereas the rest were apparently destabilizing M_{TOT} . Most of the other two-finger PCs (>81%) apparently contributed to M_{TOT} stabilization across the *Unstable* conditions, whereas <5% of those contributed to M_{TOT} stabilization in the *Stable* condition. When other two-finger PCs were considered, <5% of those (1 of 22 cases) apparently contributed to total moment of force stabilization in the *Stable* condition, whereas this was true in 35 of 43 cases (81.4%) under the *Unstable* conditions. All the observed three-finger PCs could potentially contribute to M_{TOT} stabilization.

DISCUSSION

This has been an exploratory study of adjustments in patterns of covariation of signals to fingers when a secondary task was presented on the background of an explicit primary task (constant total force production). The three general questions formulated in the INTRODUCTION received at least tentative answers in the experiments. In the absence of a secondary task (*Stable* conditions), the subjects demonstrated a wide variety of covariation patterns among finger modes compatible with the required total force level (within the uncontrolled manifold computed for the total force, UCM_F). So, there seem to be no clearly preferred directions within the UCM_F and no default patterns of finger mode covariation. The subjects used the versatility of the multifinger hand design differently to stabilize the total force. When the secondary task was introduced, indices of synergies stabilizing the total force stayed nearly unchanged. The secondary task (stabilization of the total moment of force) was dealt with by organizing new patterns of covariation among commands to the fingers within the same UCM_F . Although having two constraints imposed on a system with four variables leaves plenty of room for diverse solutions, under *Unstable* conditions the patterns of covariation became less variable and more reproducible across subjects. Two patterns were so frequent (Table 2) that they have deserved to be called *defaults*. Thus the answers to the three questions in the INTRODUCTION: Are there default patterns of covariation among elemental variables within the UCM that are common across subjects in the absence of a secondary task? Will a secondary task lead to weaker synergies stabilizing the performance variable associated with the primary task? Will a secondary task lead to less flexible (more reproducible across subjects) solutions in the space of elemental variables, particularly in the UCM subspace? are No, No, and Yes.

Stabilization of the total force and total moment of force

Although there was no explicit constraint on the total moment of force (M_{TOT}) in the *Stable* condition, one could have expected M_{TOT} stabilizing synergies based on earlier studies that reported such synergies in both discrete and cyclic tasks (Latash et al. 2001, 2002b; Scholz et al. 2002). These observations have been interpreted as suggesting that M_{TOT} stabilizing synergies represent a default pattern of finger coordination conditioned by everyday experience: for example, while taking a sip from a handheld glass, it is very important to apply an accurate rotational action, whereas the grip force can vary broadly within a relatively wide range.

All earlier studies, however, used tasks with relatively quick changes in the total force, whereas the current study involved steady-state force production. It has been noted that variance within the UCM_F (good variability) was nearly proportional to the magnitude of total force, whereas variance orthogonal to the UCM_F (bad variability) was nearly proportional to the rate of force change, dF/dt (Goodman et al. 2005; Latash et al. 2002b). This means, in particular, that steady-state tasks are expected to lead to higher indices of force-stabilizing synergies as compared with tasks that involve changes in the total force. On the other hand, synergies stabilizing the total force and total moment of force can be viewed as partly competitive. The force-stabilizing synergy favors negative covariation among forces produced by all the fingers. The moment-stabilizing synergy requires predominantly negative covariation of forces produced by fingers

acting at different sides of the pivot. It is thus possible that the steady-state nature of the task in our study led to the observations of strong force-stabilizing synergies and a lack of moment-of-force-stabilizing synergies under the *Stable* condition (see Fig. 7).

We now illustrate effects of the two constraints on possible solutions for a three-finger task (Fig. 9; note: we feel uneasy drawing four-dimensional figures). To simplify the illustration, we will also assume that enslaving is absent, such that modes and finger forces become identical. The primary task (constant total force production) corresponds to a two-dimensional subspace (UCM_F ; A–B–C in Fig. 9). Adding a secondary task (constant total moment of force) corresponds to another two-dimensional subspace (UCM_M). Intersection of the two planes produces a one-dimensional subspace. Its location depends on the location of the pivot. Two pivot locations are illustrated (Pivot-1 and Pivot-2) corresponding to two UCM_M subspaces (O–D–E and O–D–F in Fig. 9). The subspaces that satisfy both constraints are D–E and D–F lines. In this example, adding the second constraint forces the system to use a single pattern of linear covariation among the three forces (see an earlier study of pressing tasks by marginally redundant finger systems, Latash et al. 2001).

When four fingers participate in the task, intersection of UCM_F and UCM_M produces not a line but a plane. In general, there are an infinite number of pairs of linear combinations of elemental variables (PCs) that would span such a plane. Our subjects, however, showed a strong preference for two particular linear combinations that we have termed default PCs. This observation supports a hypothesis that secondary tasks can shape variability of elemental variables within the UCM computed for a variable most relevant to a primary task.

Variable solutions across subjects

Most earlier studies of multielement motor systems have focused on common features of covariation among elemental variables across subjects (reviewed in Latash et al. 2002a, 2007). However, atypical patterns of data distribution have been mentioned in several studies (Jaric and Latash 1999; Latash et al. 2001; Scholz et al. 2000). These observations have suggested that even young, healthy subjects can show different preferred patterns of solving simple motor tasks with redundant sets of effectors (Grinyagin et al. 2005; Santello and Soechting 1998). Our observations in the *Stable* condition provide more support for the use of flexible strategies across typical subjects. In the absence of an external constraint on the total moment of force (M_{TOT}), the subjects showed a wide variety of preferred patterns of covariation among the elemental variables (finger modes) within the UCM_F . Most commonly (14 of 60 occurrences), a $[1, -1, -1, 0]$ principal component was observed corresponding to a positive covariation of the M- and R-finger modes that covaried negatively with the I-finger mode. However, a variety of other covariation patterns could also be observed rather frequently. Thus in the absence of other constraints, human subjects are likely to explore different solutions compatible with the primary task formulation.

The observed variability across subjects could be related to the relative novelty of the task, although the task in the *Stable* condition was perceived by the subjects as very simple. We did not explore effects of extended practice, but it is possible that practice could lead to less variable solutions based on some optimization criteria. Such an outcome could be predicted based on results of a study of the effects of practice on a relatively simple two-hand pointing task (Domkin et al. 2002). On the other hand, the *Unstable* conditions were more challenging and novel. Nevertheless, the subjects did show more reproducible patterns without extended practice.

Lack of interference between synergies: principle of superposition

The issue of interference among synergies that share the same sets of effectors has been discussed for the past half century (Bernstein 1947, 1967). In particular, one of the hypotheses on the function of the cerebellum has been that this enigmatic structure resolves conflicts among synergies that share effectors (Bloedel 1992; Houk et al. 1996; Thach et al. 1992). Along similar lines, a principle of superposition has been suggested with respect to a variety of tasks and variables (Feldman 1986; Fingelkurts et al. 2006; Ganor and Golani 1980; Pigeon et al. 2000; Ruegg and Bongioanni 1989). This principle implies that a neural controller subdivides tasks into subtasks that are controlled independently, whereas the outputs of such subcontrollers are summed up at a hierarchically lower level.

In particular, the principle of superposition has been introduced for the prehension tasks in robotics (Arimoto et al. 2000, 2001). According to this principle, prehension tasks are controlled using two separate controllers that deal with the grip force and with the production of a required rotational hand action (total moment of force). Recent studies have suggested that the human CNS complies with the principle of superposition such that variations in the grip force and total moment of force applied to a handheld object are independent of each other (Gao et al. 2006; Latash and Zatsiorsky 2006; Shim et al. 2003, 2005; Zatsiorsky et al. 2004).

Some of the observations in our current experiments support the principle of superposition with respect to pressing tasks. In particular, when the task changed from the *Stable* to the *Unstable* condition, the index of force-stabilizing synergies did not change, whereas the index of moment-stabilizing synergies increased significantly from negative to positive values (Fig. 6). Organizing different patterns of finger mode covariation that stabilized the moment of force with respect to different pivots also had no significant effect on the index of force-stabilizing synergies—despite the significant changes in the sharing patterns (see Fig. 5). We view these observations as corroborating the principle of superposition during human multifinger tasks.

Two features of synergies

Multifinger synergies have been discussed as characterized by two major features: sharing and stability/flexibility (reviewed in Latash et al. 2007). The former feature implies that a controller uses a preferred pattern of sharing the task within a redundant set of elements (also see Li et al. 1998), whereas the second feature implies a particular pattern of covariation among elemental variables. In a recent model, the two features have been represented with two types of variables manipulated by the controller (Latash et al. 2005). This view has been supported, in particular, by observations of changes in indices of covariation without a change in the average performance of a set of elements—anticipatory synergy adjustments (ASAs; Kim et al. 2006; Olafsdottir et al. 2005; Shim et al. 2005). ASAs are seen as changes in indices of synergies in preparation for a change of a performance variable stabilized by those synergies, but before the performance variable started to change.

In our experiment, sharing patterns were substantially different across the four conditions (Fig. 5). Nevertheless, indices of force-stabilizing synergies were similar across those conditions, whereas indices of moment-stabilizing synergies were similar across the three *Unstable* conditions. This finding may be seen as complementary to ASAs in showing that control variables that define sharing patterns can be changed independently of those that define patterns of covariation among elemental variables (finger modes).

What do synergies do?

Why do people organize covariation of elemental variables when dealing with redundant motor systems? This is not necessary to solve a task or even to ensure low variability of particular performance variables. Any task can be successfully accomplished in the absence of particular

covariation patterns, simply by selecting a solution (a particular sharing pattern) and reproducing it in a stereotypical fashion. Two answers have been suggested either explicitly or implicitly. The first is that the controller deals with a particular level of “noise” in each of the elemental variables, and covariation is a method of reducing effects of this noise on variability of important performance variables (Harris and Wolpert 1998; Muller and Sternad 2003; Todorov and Jordan 2002). In other words, one of the purposes of synergies is to reduce bad variability.

This view has been supported by observations of smaller indices of relative variability (coefficients of variation) in similar tasks performed by nonredundant compared with redundant sets of effectors (Latash et al. 2001; Sosnoff et al. 2005). It has also been reflected in several models of control of redundant systems (Latash et al. 2005; Todorov and Jordan 2002).

An alternative view is that synergies do not deal explicitly with variability of performance variables but rather provide room for flexible solutions that can be used to perform other tasks or optimize features of performance not directly related to the explicit task (Latash et al. 2007; Scholz and Schöner 1999). In a few studies that compared accuracy of performance between nonredundant and redundant finger sets, the gain in accuracy in the redundant sets was between 15 and 30% (Latash et al. 2001; Sosnoff et al. 2005). Such a gain could be expected simply because of the close to linear relation between force level and its SD (reviewed in Newell et al. 1984) in the absence of any task-specific covariation among elemental variables. The apparent gain in accuracy could be due to the fact that forces produced by two effectors sum up ($F_{TOT} = F_1 + F_2$), whereas SDs do not [$SD_{TOT} < (SD_1 + SD_2)$]. According to this latter view, higher indices of synergies may reflect an increase in good variability much more than a decrease in bad variability (also see a model by Goodman and Latash 2006).

In our study, there were differences not only in indices of variance of the total force and of the total moment but also in indices of corresponding synergies across the four conditions (compare Figs. 4 and 7). However, these differences could be rather dissimilar. In particular, variance of the total force was significantly higher under the *Pivot-RL* condition than that under the *Stable* condition in the absence of differences in ΔV_F between these two conditions. On the other hand, under the *Pivot-IM* condition, variability of the total moment of force was much lower than that under all other conditions, whereas there were no differences across the three *Unstable* conditions in ΔV_M . These results corroborate an idea that indices of synergies do not necessarily reflect accuracy of performance of corresponding variables but rather other factors such as involvement of the system of effectors in secondary tasks.

Acknowledgments

We appreciated the help of Dr. Donald Richards (Department of Statistics, Penn State University).

grants

This study was supported in part by National Institutes of Health Grants AG-018751, NS-035032, AR-048563, and NS-050880.

REFERENCES

- Arimoto S, Nguyen PTA, Han HY, Doulgeri Z. Dynamics and control of a set of dual fingers with soft tips. *Robotica* 2000;18:71–80.
- Arimoto S, Tahara K, Yamaguchi M, Nguyen PTA, Han HY. Principles of superposition for controlling pinch motions by means of robot fingers with soft tips. *Robotica* 2001;19:21–28.
- Bernstein, NA. On the Construction of Movements [in Russian]. Medgiz; Moscow: 1947.

- Bernstein, NA. The Co-ordination and Regulation of Movements. Pergamon Press; Oxford, UK: 1967.
- Bloedel JR. Functional heterogeneity with structural homogeneity: how does the cerebellum operate? *Behav Brain Sci* 1992;15:666–678.
- Danion F, Schöner G, Latash ML, Li S, Scholz JP, Zatsiorsky VM. A force mode hypothesis for finger interaction during multi-finger force production tasks. *Biol Cybern* 2003;88:91–98. [PubMed: 12567224]
- Domkin D, Laczko J, Djupsjöbacka M, Jaric S, Latash ML. Joint angle variability in 3D bimanual pointing: uncontrolled manifold analysis. *Exp Brain Res* 2005;163:44–57. [PubMed: 15668794]
- Domkin D, Laczko J, Jaric S, Johansson H, Latash ML. Structure of joint variability in bimanual pointing tasks. *Exp Brain Res* 2002;143:11–23. [PubMed: 11907686]
- Doulgeri Z, Fasoulas J, Arimoto S. Feedback control for object manipulation by a pair of soft tip fingers. *Robotica* 2002;20:1–11.
- Feldman AG. Once more on the equilibrium-point hypothesis (λ -model) for motor control. *J Mot Behav* 1986;18:17–54. [PubMed: 15136283]
- Fingelkurts AA, Fingelkurts AA, Ermolaev VA, Kaplan AY. Stability, reliability and consistency of the compositions of brain oscillations. *Int J Psychophysiol* 2006;59:116–126. [PubMed: 15946755]
- Freitas SMSF, Duarte M, Latash ML. Two kinematic synergies in voluntary whole-body movements during standing. *J Neurophysiol* 2006;95:636–645. [PubMed: 16267118]
- Ganor I, Golani I. Coordination and integration in the hindleg step cycle of the rat: kinematic synergies. *Brain Res* 1980;195:57–67. [PubMed: 7397498]
- Gao F, Latash ML, Zatsiorsky VM. Control of finger force direction in the flexion-extension plane. *Exp Brain Res* 2005;161:307–315. [PubMed: 15726342]
- Goodman SR, Shim JK, Zatsiorsky VM, Latash ML. Motor variability within a multi-effector system: experimental and analytical studies of multi-finger production of quick force pulses. *Exp Brain Res* 2005;163:75–85. [PubMed: 15690155]
- Grinyagin IV, Biryukova EV, Maier MA. Kinematic and dynamic synergies of human precision grip movement. *J Neurophysiol* 2005;94:2284–2294. [PubMed: 15917316]
- Harris CM, Wolpert DM. Signal-dependent noise determines motor planning. *Nature* 1998;394:780–784. [PubMed: 9723616]
- Houk JC, Buckingham JT, Barto AG. Models of the cerebellum and motor learning. *Behav Brain Sci* 1996;19:368–383.
- Hsu WL, Scholz JP, Schöner G, Jeka JJ, Keimel T. Control and estimation of posture during quiet stand depends on multijoint coordination. *J Neurophysiol* 2007;97:3024–3035. [PubMed: 17314243]
- Jaric S, Latash ML. Learning a pointing task with a kinematically redundant limb: emerging synergies and patterns of final position variability. *Hum Mov Sci* 1999;18:819–838.
- Kilbreath SL, Gandevia SC. Limited independent flexion of the thumb and fingers in human subjects. *J Physiol* 1994;479:487–497. [PubMed: 7837104]
- Kim SW, Shim JK, Zatsiorsky VM, Latash ML. Anticipatory adjustments of multi-finger synergies in preparation for self-triggered perturbations. *Exp Brain Res* 2006;174:604–612. [PubMed: 16724179]
- 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, Li Z-M, Zatsiorsky VM. A principle of error compensation studied within a task of force production by a redundant set of fingers. *Exp Brain Res* 1998;122:131–138. [PubMed: 9776511]
- Latash ML, Scholz JP, Danion F, Schöner G. Structure of motor variability in marginally redundant multi-finger force production tasks. *Exp Brain Res* 2001;141:153–165. [PubMed: 11713627]
- Latash ML, Scholz JP, Danion F, Schöner G. Finger coordination during discrete and oscillatory force production tasks. *Exp Brain Res* 2002b;146:419–432. [PubMed: 12355270]
- Latash ML, Scholz JP, Schöner G. Motor control synergies revealed in the structure of motor variability. *Exerc Sport Sci Rev* 2002a;30:26–31. [PubMed: 11800496]
- Latash ML, Scholz JP, Schöner G. Toward a new theory of motor synergies. *Motor Control* 2007;11:276–308. [PubMed: 17715460]
- Latash ML, Shim JK, Gao F, Zatsiorsky VM. Rotational equilibrium during multi-digit pressing and prehension. *Motor Control* 2004;8:392–404. [PubMed: 15585896]

- Latash ML, Shim JK, Smilga AV, Zatsiorsky VM. A central back-coupling hypothesis on the organization of motor synergies: a physical metaphor and a neural model. *Biol Cybern* 2005;92:186–191. [PubMed: 15739110]
- Latash ML, 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. *Exp Brain Res* 2003;151:60–71. [PubMed: 12740728]
- Latash ML; Zatsiorsky VM. Principle of superposition in human prehension. In: Kawamura, S.; Swinin, M., editors. *Advances in Robot Control: From Everyday Physics to Human-Like Movements*. Springer; New York: 2006. p. 249–261.
- Li ZM, Latash ML, Zatsiorsky VM. Force sharing among fingers as a model of the redundancy problem. *Exp Brain Res* 1998;119:276–286. [PubMed: 9551828]
- Loeve, M. *Probability Theory*. 4th ed.. Vol. I. Springer; New York: 1977.
- Ohtsuki T. Inhibition of individual fingers during grip strength exertion. *Ergonomics* 1981;24:21–36. [PubMed: 7227358]
- Olafsdottir H, Zhang W, Zatsiorsky VM, Latash ML. Age-related changes in multifinger synergies in accurate moment of force production tasks. *J Appl Physiol* 2007;102:1490–1501. [PubMed: 17204576]
- Parra-Vega V, Rodriguez-Angeles A, Arimoto S, Hirzinger G. High precision constrained grasping with cooperative adaptive handcontrol. *J Intell Robot Syst* 2001;32:235–254.
- Pigeon A, Yahia LH, Mitnitski AB, Feldman AG. Superposition of independent units of coordination during pointing movements involving the trunk with and without visual feedback. *Exp Brain Res* 2000;131:336–349. [PubMed: 10789948]
- Ruegg DG, Bongioanni F. Superposition of ballistic on steady contractions in man. *Exp Brain Res* 1989;77:412–420. [PubMed: 2792287]
- Santello M, Soechting JF. Gradual molding of the hand to object contours. *J Neurophysiol* 1998;79:1307–1320. [PubMed: 9497412]
- 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]
- Scholz JP, Reisman D, Schöner G. Effects of varying task constraints on solutions to joint coordination in a sit-to-stand task. *Exp Brain Res* 2001;141:485–500. [PubMed: 11810142]
- Scholz JP, Schöner G. The uncontrolled manifold concept: identifying control variables for a functional task. *Exp Brain Res* 1999;126:289–306. [PubMed: 10382616]
- Scholz JP, Schöner G, Latash ML. Identifying the control structure of multijoint coordination during pistol shooting. *Exp Brain Res* 2000;135:382–404. [PubMed: 11146817]
- Schöner G, Scholz J. Analyzing variance in multi-degree-of-freedom movements: uncovering structure versus extracting correlations. *Motor Control* 2007;11:259–275. [PubMed: 17715459]
- Shim JK, Latash ML, Zatsiorsky VM. Prehension synergies: trial-to-trial variability and hierarchical organization of stable performance. *Exp Brain Res* 2003;152:173–184. [PubMed: 12898101]
- Shim JK, Lay B, Zatsiorsky VM, Latash ML. Age-related changes in finger coordination in static prehension tasks. *J Appl Physiol* 2004;97:213–224. [PubMed: 15003998]
- 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]
- Thach WT, Goodkin HG, Keating JG. Cerebellum and the adaptive coordination of movement. *Ann Rev Neurosci* 1992;15:403–442. [PubMed: 1575449]
- Todorov E, Jordan MI. Optimal feedback control as a theory of motor coordination. *Nat Neurosci* 2002;5:1226–1235. [PubMed: 12404008]
- Zatsiorsky VM, Gao F, Latash ML. Prehension synergies: effects of object geometry and prescribed torques. *Exp Brain Res* 2003;148:77–87. [PubMed: 12478398]
- Zatsiorsky VM, Latash ML, Gao F, Shim JK. The principle of superposition in human prehension. *Robotica* 2004;22:231–234.
- Zatsiorsky VM, Li ZM, Latash ML. Coordination force production in multi-finger tasks: finger interaction and neural network modeling. *Biol Cybern* 1998;79:139–150. [PubMed: 9791934]

- Zhang W, Zatsiorsky VM, Latash ML. Accurate production of time-varying patterns of the moment of force in multi-finger tasks. *Exp Brain Res* 2006;175:68–82. [PubMed: 16779549]
- Zhang W, Zatsiorsky VM, Latash ML. Finger synergies during multi-finger cyclic production of moment of force. *Exp Brain Res* 2007;177:243–254. [PubMed: 16944107]

Fig. 1.

The experiment setup. *A*: examples of the templates and subject's performance shown on the screen during the experiment. *B, left*: the subject and arm positions. *Right*: the *Stable* and *Unstable* force-producing condition setup. Under the *Unstable* condition, the plate with the force sensors rested on a pivot between the Index (I) and Middle (M), between the Middle (M) and Ring (R), or between the Ring (R) and Little (L) fingers. A counterload was used in the *Pivot-IM* and *Pivot-RL* conditions to balance the plate with the sensors in the absence of finger forces. *C*: front view of the plate with the sensors resting on the pivot. An inverted-T-shape bar was fitted into one of 3 grooves under the plate with the sensors.

Fig. 2.

The time profiles of total force (F_{TOT}) during the 4 conditions (*Stable*, *Pivot-IM*, *Pivot-MR*, and *Pivot-RL*) in the steady-state task performed by a typical subject. Each panel represents the subject's total force performance in the 24 trials.

Fig. 3.

The time profiles of the total moment of force (M_{TOT}) during the 4 conditions (*Stable*, *Pivot-IM*, *Pivot-MR*, and *Pivot-RL*) in the steady-state task performed by a typical subject. For the *Stable* condition, M_{TOT} was computed with respect to a pivot location at midpoint between the M and R fingers.

Fig. 4. Normalized variance of F_{TOT} ($V_{F,N}$, A) and M_{TOT} ($V_{M,N}$, B) averaged across subjects with SE bars. $V_{F,N}$ and $V_{M,N}$ were computed across trials for each condition for each subject and averaged over 200-ms time windows in the middle of each of the steady-state force intervals. These indices were normalized by each subject's $(MVC_{IMRL})^2$ and $(0.03MVC_{IMRL})^2$, and are thus dimensionless, and further averaged across subjects. The 3 force levels (5, 7.5, and 10% MVC) are shown on the x -axis; the 4 different conditions are indicated by different bar patterns. Symbol * indicates significant differences between conditions.

Fig. 5.

Sharing patterns, averaged across subjects, of the total force among individual fingers (S_I , S_M , S_R , S_L) under *Stable* (A), *Pivot-IM* (B), *Pivot-MR* (C), and *Pivot-RL* (D) conditions. S_i indices were computed for each time sample of each trial under each condition for each finger of each subject. Further, these indices were averaged across trials, over 200-ms time windows, in the middle of each force interval under each condition, across the 3 force levels under each condition and across subjects. White slices represents the I finger share, S_I ; black slices represent the M finger share, S_M ; light gray slices represent the R finger share, S_R ; and the grid slices represent the L finger share, S_L .

Fig. 6.

Typical time profiles of ΔV indices (dimensionless) for the total force (ΔV_F , A) and the total moment of force (ΔV_M , B) under the 4 conditions for a typical subject. The 3 force levels within each trial are indicated by dotted vertical lines and horizontal arrows. The 4 lines represent ΔV indices under the 4 conditions: *Stable*, solid lines; *Pivot-IM*, dashed lines; *Pivot-MR*, dotted lines; and *Pivot-RL*, dash-dotted lines.

Fig.7.

ΔV indices (dimensionless), averaged across subjects, for the total force (ΔV_F , A) and the total moment of force (ΔV_M , B) for the 3 force levels and 4 task conditions with SE bars. The ΔV indices were averaged over 200-ms time windows in the middle of each of the steady-state force intervals and further averaged across subjects. For each force level, 4 different bar patterns represent 4 conditions: *Stable*, empty bars; *Pivot-IM*, striped bars; *Pivot-MR*, solid bars; and *Pivot-RL*, grid bars.

Fig. 8.

A schematic illustration of the 2 “default PCs” and 3-finger PCs as derivatives from the 2 default PCs. Significantly loaded finger modes are shown by gray or black fingers. Similar shadings refer to similar signs of the loading coefficients, whereas different shadings refer to opposite signs. The numbers in square brackets represent loading coefficients with 1 and -1 standing for loading coefficients with the absolute magnitude >0.5 ; 0 stands for all other loading coefficients.

Fig. 9.

An illustration of the uncontrolled manifold (UCM) for the total force (UCM_F) and total moment of force (UCM_M) for a 3-finger force-production task and 2 locations of the pivot (Pivot-1 and Pivot-2). An interaction of 2 UCMs corresponds to force values that stabilize both the total force and the total moment (lines DF and DE). Note that no enslaving has been assumed in this illustration.

Table 1

Loading factors for the within-UCM_F PCA

Force Level	Task											
	Stable				Pivot-IM				Pivot-MR			
	PC1'	PC2'	PC1'	PC2'	PC1'	PC2'	PC1'	PC2'	PC1'	PC2'	PC1'	PC2'
F ₁												
Loading factors	-0.69	0.24	-0.59	-0.03	-0.17	0.83	0.35	0.58	-0.60	-0.20	-0.75	0.24
Variance explained	51.6%	27.7%	54.2%	36.1%	49.8%	46.1%	45.5%	44.5%				
F ₂												
Loading factors	-0.58	0.37	-0.65	-0.04	-0.79	0.11	0.61	0.36	-0.63	0.10	-0.76	0.53
Variance explained	50.6%	31.7%	52.9%	40.5%	49.0%	48.4%	47.3%	36.9%				
F ₃												
Loading factors	-0.58	0.36	-0.65	-0.01	-0.80	0.14	-0.67	-0.25	0.69	-0.29	0.70	-0.60
Variance explained	49.3%	31.4%	49.0%	42.3%	50.1%	47.4%	41.5%	38.0%				

The loading factors and percentages of the total variance explained by each factor are presented for the three force levels (F₁, F₂, and F₃) and for the four tasks for a typical subject. Significant loading factors (>0.5) are shown in bold.

Table 2

Numbers of occurrences of different types of PCs

PC Type	Loading Factor	Stable	Pivot-IM	Pivot-MR	Pivot-RL	Total
Two-finger PC	[1 -1 0 0]	6	13	28	11	58
	[0 0 -1 1]	3	14	27	8	52
	[0 1 -1 0]	2	11		7	19
	[1 0 -1 0]	6	1		7	14
	[0 1 0 -1]	7	2	1	1	11
Three-finger PC	[1 0 0 1]					
	[1 0 0 -1]	3	5		5	5
	[0 1 0 1]				3	3
	[0 0 1 1]	3				3
	[0 1 1 0]	1				1
	[1 -1 -1 0]	14			2	16
	[1 -1 0 -1]	2			1	3
	[1 -1 1 0]		1			1
	[1 -1 0 1]		3			3
	[-1 0 -1 1]		3			3
One-finger PC	[0 -1 -1 1]	1	1	1		3
	[0 1 -1 1]				4	4
	[1 0 -1 1]				2	2
	[1 0 0 0]			2	3	5
	[0 1 0 0]		1		3	4
	[0 0 1 0]	2	3	1		6
	[0 0 0 1]	10	3		3	16

The total number of occurrences of different types of PCs are presented across all subjects, tasks, and force levels. In the second column, loading factors with the absolute magnitude >0.5 are represented as 1 or -1; loading factors with the absolute magnitude <0.5 are represented as 0. Note the very frequent occurrences of the first two PCs (default PCs), particularly in the *Pivot-MR* condition.