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Prehension of Half-Full and Half-Empty Glasses: Time and History Effects on Multi-Digit Coordination

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Abstract

We explored how digit forces and indices of digit coordination depend on the history of getting to a particular set of task parameters during static prehension tasks. The participants held in the right hand an instrumented handle with a light-weight container attached on top of the handle. At the beginning of each trial, the container could be empty, filled to the half with water (0.4 l) or filled to the top (0.8 l). The water was pumped in/out of the container at a constant, slow rate over 10 s. At the end of each trial, the participants always held a half-filled container that has just been filled (Empty-Half), emptied (Full-Half), or stayed half-filled throughout the trial (Half-Only). Indices of co-variation (synergy indices) of elemental variables (forces and moments of force produced by individual digits) stabilizing such performance variables as total normal force, total tangetial force, and total moment of force were computed at two levels of an assumed control hierarchy. At the upper level, the task is shared between the thumb and virtual finger (an imagined digit with the mechanical action equal to that of the four fingers), while at the lower level, action of the virtual finger is shared among the actual four fingers. Filling or emptying the container led to a drop in the safety margin (proportion of grip force over the slipping threshold) below the values observed in the Half-Only condition. Synergy indices at both levels of the hierarchy showed changes over the Full-Half and Empty-Half condition. These changes could be monotonic (typical of moment of force and normal force) or non-monotonic (typical of tangential force). For both normal and tangential forces, higher synergy indices at the higher level of the hierarchy corresponded to lower indices at the lower level. Significant differences in synergy indices across conditions were seen at the final steady-state showing that digit coordination during steady holding an object is history dependent. The observations support an earlier hypothesis on a trade-off between synergies at the two levels of a hierarchy. They also suggest that, when a change in task parameters is expected, the neural strategy may involve producing less stable (easier to change) actions. The results suggest that synergy indices may be highly sensitive to changes in a task variable and that effects of such changes persist after the changes are over.

Introduction

Prehension synergies have been defined as co-varied adjustments of forces and moments of force produced by individual digits across repetitive attempts at static tasks of holding an object (reviewed in Zatsiorsky and Latash 2004, 2008). This definition makes prehension synergies a member of a broader class of motor synergies defined based on the principle of abundance (Gelfand and Latash 1998). The principle of abundance views the redundant design of the neuromotor system, typical of all the levels of movement analysis (Bernstein 1967), not as the source of computational problems for the central nervous system (CNS) but as a rich mechanism that ensures both movement stability and flexibility (adaptive

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behavior to perturbations, both internal and external, changes in task goals, and secondary tasks). Several recent studies (reviewed in Latash 2010) have shown that redundant (abundant) systems show stable performance under such manipulations as fatigue of one of the elements (Singh et al. 2010a), expected and unexpected external perturbations (Scholz et al. 2000; Gorniak et al. 2010c), and addition of a secondary task constraint (Zhang et al. 2008; Singh et al. 2010b). Within this framework, synergies are defined as neural organizations that ensure co-variation of variables produced by elements of a redundant, multi-element system that stabilizes a desired value (time profile) of a potentially important performance variable to which all the elemental variables contribute.

Synergies have been quantified within the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999; reviewed in Latash et al. 2002b, 2007). The UCM hypothesis views motor tasks as being performed within a space of elemental variables (for example forces and moments of force produced by each of the digits). The controller organizes in that space a subspace (UCM) corresponding to a desired value of a potentially important performance variable (for example, resultant force or resultant moment of force) produced by all the elements together and then it limits variance of elemental variables primarily to the UCM. Analysis within the UCM hypothesis commonly involves quantifying two components of variance in the space of elemental variables, one that leads to changes in a selected performance variable ("bad" variance, V_{BAD}), and the other that does not ("good" variance, V_{GOOD}). For example, variance in finger force space computed across trials at a certain phase of an action may be viewed as consisting of two components, preserving the average across trials value of the total force (V_{GOOD} with respect to total force) and modifying total force (V_{BAD}). In some studies, these two indices are reduced to a single metric reflecting the relative amount of V_{GOOD}.

Earlier studies of prehension synergies focused primarily on co-varied patterns of elemental variables that stabilize such performance variables as grip force, load-resisting force, and total moment of force at specific phases of the actions (reviewed in Zatsiorsky and Latash 2008; Latash and Zatsiorsky 2009; Latash et al. 2010). Indices of synergies, however, have been shown to be sensitive to the rate of change of the performance variable (Latash et al. 2002a; Shim et al. 2005; Friedman et al. 2010). In particular, in experiments when a performance variable represented a weighted sum of elemental variables (such as total force or total moment of force), the amount of V_{GOOD} has been found to be sensitive to the magnitude of the performance variable while the amount of V_{BAD} was proportional to the rate of change of that variable. The latter finding has been interpreted as a reflection of a relative timing error across trials (Latash et al. 2002a; Goodman et al. 2005).

Prehension synergies have been studied at two levels of a hypothetical control hierarchy (Arbib et al. 1985). At the upper level of the hierarchy, the task is shared between the actions of the thumb (TH) and the virtual finger (VF, an imagined digit that produces the same mechanical effects as all the fingers together). At the lower level the action of the thumb is shared among the individual fingers (IFs). Correspondingly, elemental variables at the upper level are forces and moments of force produced by the thumb and VF. At the lower level, elemental variables are those produced by the fingers while VF output is the performance variable. A series of earlier studies have shown a trade-off between synergy indices at the two levels (Gorniak et al. 2007a,b, 2009a,b): High synergy indices at the higher level (VF–TH level) are commonly associated with low synergy indices at the lower level (IF level). The cited studies have shown that this trade-off is partly inherent to the method of computation of the synergy indices, but that the trade-off is not absolute and can be overcome by the neural controller, i.e. it reflects motor control processes.

In this study, we focused on features of prehension synergies that reflect history of getting to a particular set of performance variables. This issue has not been studied although history dependence of a variety of neuromotor phenomena, such as contractile properties of muscles and parameters of spinal reflexes, have been documented (Partridge 1965; Gielen et al. 1984; Kostyukov 1998). So, we hypothesized that synergy indices would differ between conditions that include performing the same task starting from different values of task parameters. Since history effects on synergy indices have not been studied, we cannot be more specific about predicted changes. We can, however, hypothesize that a condition characterized by higher synergy indices at one of the levels of the hierarchy would show lower synergy indices at the other level (see Gorniak et al. 2009b).

To study such effects, we used a task of holding steadily a handle (a task studied extensively before, reviewed in Zatsiorsky and Latash 2004, 2008) with a container that was always filled with water to the middle of its volume by the end of each trial, while the starting conditions varied from empty, to half-full, to full. To minimize possible effects of the rate of change of performance variables on synergy indices (Shim et al. 2005; SKM et al. 2010), we purposefully used very slow changes in the amount of water (load). Nevertheless, we could not discard a possibility that there will be modest time modulation of the synergy indices proportional to the non-zero rate of change of the weight of the handle with the container.

We also explored other characteristics of prehension such as the normal and tangential forces and the safety margin (SM) defined as the proportion of grip force over the slipping threshold (Johansson and Westling 1984; Pataky et al. 2004). There have been inconclusive reports on possible dependence of the safety margin on the rate of force change (Flanagan and Wing 1995; Zatsiorsky et al. 2004, Jaric et al. 2006). To avoid this problem, we used very slow changes in the weight of the object. No studies investigated dependence of these variables on history of load change; so, this was pure exploration.

Methods

Participants

Five male and three female subjects participated in this study. Average data for the males were 26±4 years of age, 1.73±0.08 m in height, 67.24±7.04 kg in weight, 8.70±0.27 cm in right hand width and 18.90±0.89 cm in right hand length. Average data for the females were 28±6 years of age, 1.57±0.03 m in height, 63.37±10.3 kg in weight, 7.77±0.25 cm in right hand width and 17.93±1.21 cm in right hand length. Hand width was measured between the lateral aspects of the index and little finger metacarpophalangeal (MCP) joints. Hand length was measured as the distance from the tip of the distal phalanx of the middle finger to the distal crease of the wrist with the hand in a neutral flexion/extension pose. All subjects were strongly right-handed and had no previous history of neuropathies or traumas to the upper limbs. Handedness was assessed by the subjects' preference during their daily writing and eating. None of the subjects had a history of long-term involvement in hand or finger professional activities such as typing or playing musical instruments. All subjects gave informed consent according to the procedures approved by the Office of Regulatory Compliance of the Pennsylvania State University.

Experimental setup

Five six-component force–moment transducers (four Nano-17 for the four fingers and one Nano-25 for the thumb; ATI Industrial Automation, Garner, NC, USA) were mounted on a handle made of aluminum (Figure 1, right panel). The center points of two of the Nano-17 sensors were 0.03 and 0.01 m above the midpoint of the handle, respectively. The center points of the remaining two Nano-17 sensors were 0.01 and 0.03 m below the midpoint of the handle, respectively. The Nano-25 sensor was located at the midpoint of the handle. The centers of all the sensors were within one plane referred to as the grasp plane.

A circular metal plate, 0.17 m in diameter and 0.01 m in height was attached to the top of the handle for placing the water container (Figure 1, left panel). A plastic wide mouth bottle with maximum volume of 1 L was used as the water container. The top surface of the circular metal plate and the bottom of the plastic bottle were fitted with Velcro pieces such that no movement of the bottle with respect to the handle was possible during the experiment. To keep the bottle on the handle with the same position and orientation at all time, two lines were marked on the top of plate. A circular bulls-eye level with 2° tolerance was placed on the circular plate next to the bottle as a feedback device for the subject to keep the handle orientation vertical at all times.

A variable flow chemical pump (VWR LabShop, Batavia, IL, USA) was used for emptying or filling the bottle during the experiment. The speed of the flow was kept constant at a value to about 0.04 liter/s; so, the total time of pumping 400 ml of water in/out was close to 10 s. The plastic tube connecting the pump and the bottle went through a funnel fastened onto the mouth of the bottle to keep the opening of the tube in the center of the bottle. The tube was handled by an experimenter to make sure that its weight did not add to the weight of the container.

The total mass of the handle with five sensors, the empty bottle and the funnel was 0.497 kg. Sandpaper (100-grit) was attached to the contact surface of each sensor to increase the friction between the digits and the transducers. Similarly to earlier studies (Shim et al. 2003, 2004; Gorniak et al. 2009a,b), such very high friction was used to ensure that the subjects did not have to apply large grip forces that might introduce individual differences related to individual digit strength.

Transducer signals were amplified and multiplexed using a customized conditioning box (from ATI Industrial Automation) prior to being routed to a 12-bit analog to digital converter (PCI-6225, National Instruments, Austin, TX, USA). A customized Labview program (National Instruments, Austin, TX, USA) was used for data acquisition and customized MATLAB (Mathworks Inc., Natick, MA, USA) programs were written for data processing. Signals were sampled at 200 Hz.

Procedure

Subjects sat with an erect posture, arms unsupported, facing the apparatus. They were asked to use the right hand to hold the handle with each digit tip placed on the center of the corresponding sensor. When holding the handle, the subject's right upper arm was abducted at approximately 45° in the frontal plane and internally rotated approximately 30° degrees, the elbow was flexed approximately 45°, and the wrists was in a neutral supination-pronation position with the thumb facing the midline of the body. The left hand rested on the lap. The distance between the right hand and the chest was approximately 25 cm.

There were three conditions in this study, the volume of water could be: 1) always 400 ml (Half-Only); 2) changed from 0 ml to 400 ml (Empty-Half); and 3) changed from 800 ml to 400 ml (Full-Half). Before each trial, the signals from the sensors were set to zero. Subjects were instructed not to touch the sensors during the zeroing process. During the recording, subjects were asked to keep the handle steadily without deviations from the vertical (keeping the air bubble in the center of the level) until they heard a beep indicated that the trial was over. The duration of each trial was 15 s in the Half-Only condition (only 5 s in one of the subject), and 20 s in the Empty-Hall and Full-Empty conditions. The shorter duration of the Half-Only trials was used to decrease the duration of the experiment; note that the data in those trials were effectively reduced to only one point – see later. In the Empty-Half and Full-Half conditions, the subject held the handle with the bottle steadily for the first 3-4s, and then the experimenter turned on the pump to pump the water in/out of the bottle at a constant speed. Once the water level reached the mark of 400 ml, the experimenter turned the pump off, while the subject continued to hold the handle vertically for another 3-4 s till the end of trial. The subjects looked at the bottle and the level at all times. After each trial, the experimenter drained or filled the bottle to its initial state. Subjects took a rest after each trial and between condition. The intervals after each trial were about 30 s and the intervals between conditions were about 5min. There were 24 trials for each condition for a total of 72 trial. The order of the conditions for each subject was created by random permutation. The same order could not be repeated more than three times.

Data processing

In each trial of the Empty-Half and Full-Half conditions, the total tangential force of all five digits, F^t_{TOT} was determined within the steady holding phases preceding (1.5-2 s) and following (18.5-19 s) water pumping. The mean F^t_{TOT} and its standard deviation were computed over the samples within each steady-state. The first time point which differed from the mean F^t_{TOT} by more than two standard deviations computed from the first steady-state was defined as the start point of load change, t_{START}. The last point that was out of the same range for the second steady-state was defined as the completion point of the load change, t_{END}. The data between t_{START} and t_{END} were filtered at 10 Hz with using a second-order, zero-lag Butterworth filter and re-sampled to 100 points. For each dependent variable, the data were also averaged over 0.5 s time intervals within the steady-state starting 0.5 s away from t_{START} and t_{END}, respectively. As a result, 102 values were obtained for each variable within each trial. For the Half-Only condition, the data from 3 s to 6 s (from 2 s to 5 s for the only subject who held the handle for 5 s) were low-pass filtered and re-sampled in the same way for further analysis.

Digit forces and moments of force were computed within sensor-based reference frames for individual sensors with the axes referred to as x_j (horizontal axis in a sagittal plane), y_j (vertical axis), and z_j (normal force direction) (where $j = th, i, m, r$, and l referring to the thumb, index, middle, ring, and little fingers, respectively). Note that the thumb x_{th} and z_{th} axes are in the opposite direction as compared to the axes of the finger sensors. Net force and net moment of force used in the following analysis were computed within the handle-based reference frame (X, Y, Z) with respect to the geometric center of the handle, X,Y,Z = 0. To compute the moment of force in the handle-based reference frame, the center of pressure coordinates for each sensor, COP_y, were computed using the equations for the point of wrench application (Zatsiorsky 2002):

$$COP_y = M_x / F_z.$$

The slip safety margin (SM, the proportion of grip force over the slipping threshold; Johansson and Westling, 1984; Burstedt et al. 1999; Pataky et al. 2004) for the thumb was computed as:

$$SM = \frac{\left(F^n_{TH} - \left|F^t_{TH}\right| / \mu\right)}{F^n_{TH}} \quad (1)$$

where F^n is the normal force applied to the object, F^t is the tangential (load-bearing) force, and μ is the coefficient of static friction between the finger pad and sandpaper interface. Since the thumb normal force was close to the VF normal force (see below) the thumb normal force was selected to represent the grip force. The maximum value for SM is unity if no load-bearing force (F^t) is exerted on the object and the minimum value for SM is zero if just enough force is exerted on the object to prevent slipping. To decrease the time of the experiment, we did not measure individual friction coefficients but assumed $\mu = 1.4$ based on earlier studies (Zatsiorsky et al. 2002; Aoki et al. 2006; Savescu et al. 2008).

Variance Analysis

Variance analyses were performed at two levels of the assumed control hierarchy: the virtual finger-thumb level (VF–TH level) and the individual finger level (IF level) (Arbib et al. 1985; Iberall 1987). VF stands for an imagined digit with the mechanical action equal to the combined action of the four fingers. At the VF–TH level, the output of the VF and thumb were analyzed. At the IF level, the outputs of each individual finger within the VF were analyzed (namely IMRL).

At the IF level, the variables included the normal forces of each individual finger (F^n_j; $j = i, m, r$, and l), the tangential forces of each individual finger (F^t_j), and the moments produced by the fingers (M_j). At the VF–TH level, the variables included the normal, tangential, and resultant forces of the VF and thumb (F^n_{VF}, F^n_{TH}, F^n_{TOT}, F^t_{VF}, F^t_{TH}, F^t_{TOT}) as well as the moments of force (M_{VH}, M_{TH}, M_{TOT}).

A total of 22 values for each variable in each trial were used for variance analysis. The first and last values were from the initial and final steady-states, PRE and POST. The other 20 values were sampled from the 100 values between t_{START} and t_{END}, evenly spread. The indices of co-variation of elemental variables (forces and moments of force produced by individual digits) were computed at each of the two levels, VF–TH and IF, for each sample across the 24 trials for each condition and each subject separately. Each index, ΔV, was computed as the difference between the sum of the variances of elemental variables [ΣVar(EV)] and the variance of the total output of these elemental variables [Var(ΣEV)]. Further, ΔV was normalized by ΣVar(EV) to allow comparisons across conditions and subjects:

$$\Delta V = \frac{\Sigma Var(EV) - Var(\Sigma EV)}{\Sigma Var(EV)} \quad (2)$$

Specifically, six indices were computed as:

$$\Delta V(i_{VF-TH}) = \frac{Var(i_{VF}) + Var(i_{TH}) - Var(i_{TOT})}{Var(i_{VF}) + Var(i_{TH})} \quad (3)$$

$$\Delta V(i_{IF}) = \frac{\Sigma Var(i_j) - Var(i_{VF})}{\Sigma Var(i_j)} \quad (4)$$

where i stands for F^n, F^t, and M.

Positive values of ΔV reflect predominantly negative co-variation among forces (or moments of force) produced by either the thumb and VF (equations 3-5) or by the individual digits (equations 6-8). We interpret ΔV > 0 as sign of a force (or moment of force) stabilizing synergy (Shim et al. 2005; Gorniak et al. 2009b). Large positive ΔV values correspond to larger amounts of negative co-variation, thus a stronger synergy. A result of ΔV = 0 implies independent variation of digit forces, and correspondingly the absence of a synergy, while ΔV < 0 may be interpreted as co-variation of elemental variables destabilizing their combined output. The normalization limits the value of ΔV by +1 for perfect force stabilizing synergies (the individual elemental variables vary across trials but variance of the performance variable equals zero) and by –1 or –3 at the VF-TH level and IF level respectively. For the Half-Only condition, the average ΔV for each variable was calculated for comparison with the final steady-state in the other two conditions.

Statistics

Standard methods of parametric statistics were used, and the data are presented as means and standard errors.

Two types of analyses were run. First, to study possible effects of history on outcome variables such as SM, forces, moments of force, and indices of synergies, a one-way repeated-measures ANOVA was applied to the values of those variables measured at the POST state with the factor *Condition-1* (three levels, Half-Only, Empty-Half, and Full-Half). Second, to study possible changes in the mentioned variables in the process of adding or removing weight, a two-way repeated-measures ANOVA was used with the factors *Condition-2* (two levels, Empty-Half, and Full-Half) and *Time* (three levels, PRE, Middle, and POST).

Before statistical analysis of the SM and synergy indices, the data were subjected to Fisher's z-transformation modified to fit the limits inherent to these variables. Pair-wise comparisons were performed with Bonferroni corrections to further analyze significant effects of ANOVAs. The Greenhouse-Geisser criterion was used to adjust degrees-of-freedom if the data violated the sphericity assumption; p-values for significance were set as 0.05.

Results

Analysis of Mechanical Variables

Overall, the subjects maintained an orientation of the handle close to the vertical at all times. This was reflected at close to zero total normal force (F^n_{TOT}), close to the weight of the object total tangential force (F^t_{TOT}), and close to zero total moment of force (M_{TOT}). On average, across subjects and conditions, at the final steady-state (POST), F^n_{TOT} was -0.14 ± 0.10 N, M_{TOT} was –1.63 ±0.56 Ncm (negative sign indicates supination moment), and F^t_{TOT} at final steady-state was 8.71±1.82 N.

In the Empty-Half and Full-Half conditions, normal forces, F^n of all digits changed smoothly with the induced changes in the weight of the object. At the final steady-state, there were no significant differences across the three conditions (including the Half-Only one) as confirmed by the one-way repeated measure ANOVA. There were also changes in F^t_{TOT} with the weight of the object in the Empty-Half and Full-Half conditions. The magnitude of these changes was 3.56 ± 0.09 N in the Empty-Half condition and 3.68 ± 0.09 N in the Full-Half condition.

Figure 2 illustrates the time profiles of the forces produced by the thumb and virtual finger (VF) averaged across subjects in the Empty-Half (solid traces) and Full-Half (dashed traces) conditions. The data for the Half-Only condition are shown aligned with the POST time sample. Note the smooth, slow changes in both normal and tangential forces. The average peak rate of total F^t was 0.54 ± 0.026 N/s, while for F^n of the thumb it was 1.56 ± 0.25 N/s. The time profiles of forces were irregular with the force peak occurring in different subjects within a wide range, from 2% to 69% of the total time. At the POST state, the tangential forces were very similar across the three conditions. On average, the normal forces, were higher for the Half-Only condition. However, these differences were not statistically significant because of the large across-subjects variability (one-way ANOVA with *Condition-1* as a factor).

Changes in all the force variables with time have been confirmed with a two-way ANOVA, *Condition-2* × *Time*, which showed effects of *Condition-2* ($F_{1,7} > 84.0$; $p < 0.001$) and a significant *Condition-2* × *Time* interaction ($F_{1.17–2,14} > 190.0$; $p < 0.001$) for each of the four force variables. The effect of *Condition-2* reflected the higher forces in the Full-Half condition, while the interaction reflected the changes in forces in opposite directions with time under the two conditions. In addition, there were significant effects of *Time* on the normal forces produced by both the thumb and VF ($F_{1.04,7.25} > 24.0$; $p < 0.01$) corresponding to higher forces at the PRE state as compared to the middle of the trial and POST state.

Moments of force produced by the thumb and VF also showed smooth changes with the load (illustrated in Figure 3). These changes were in opposite directions such that the total moment of force remained close to zero at all time. At the PRE state, the magnitudes of the moment of force produced by the thumb and VF were higher in the Full-Half condition than in the Empty-Half condition. At the POST state, the magnitudes did not differ across the three conditions. A two-way ANOVA, *Condition-2* × *Time*, confirmed effects of *Condition-2* on each moment variable ($F_{1,14} > 265$; $p < 0.001$) and a significant *Condition-2* × *Time* interaction ($F_{2,14} > 366$; $p < 0.001$). The effects of *Condition-2* reflected the overall higher thumb and VF moment of force magnitudes for the Full-Half condition, while the interaction reflected the changes in the moments of force in opposite directions under the two conditions.

Safety Margin

Safety margin (SM) was computed as the amount of grip force exerted beyond what was necessary to prevent object slipping (see Methods). Figure 4 illustrates changes in SM for a typical subject (panel A) and also averaged across subjects values after *z*-transformation (SM_Z, panel B). Note the drop in SM with time in both Full-Half and Empty-Half condition. At the final steady-state (POST), the safety margin for the Half-Only condition was the highest.

These results were supported by two ANOVAs. One-way ANOVA on SM_Z at POST showed a significant effect of *Condition-1* ($F_{1.65,11.63} = 4.635$; $p < 0.05$) followed by pair-wise contrasts with Bonferroni corrections. Two-way ANOVA, *Condition-2* × *Time*, showed significant effect of *Time* ($F_{1.06,7.43} = 45.7$; $p < 0.001$), and a significant *Condition-2* × *Time* interaction ($F_{1.26,8.8} = 36.6$; $p < 0.001$). Pair-wise comparisons with Bonferroni corrections confirmed significant ($p < 0.05$) differences across all three time samples (PRE, Middle, and POST) for the Empty-Half condition and significant differences between the POST vs. Middle and POST vs. PRE for the Full-Half condition.

Analysis of the Co-variation Index

Variance indices of all the mechanical variables were computed across all the trials for each time sample (after resampling to 20 points), each condition, and each subject separately. Further, an index of co-variation, ΔV was computed reflecting the normalized difference between the sum of the variances of elemental variables and the variance of their combined output for each of the two levels of the assumed hierarchy, VF-TH and IF (see Methods). The ΔV indices were subjected to the Fischer z-transformation adjusted to the limits of those variables before statistical analyses. The averaged across subjects ΔV_Z values are shown in Figure 5.

VF-TH Level—At the VF-TH level (outputs of the thumb and VF are viewed as elemental variables), $\Delta V_Z > 0$ for all three major variables, F^n, F^t, and M_{TOT}, in all three conditions and at all times. Note that $\Delta V_Z > 0$ implies co-variation among elemental variables that reduces variance of their combined output as compared to what could be expected in the absence of co-variation. In other words, $\Delta V_Z > 0$ means a synergy stabilizing the performance variable for which the index was computed. In the Full-Half and Empty-Half conditions $\Delta V_Z\left(F^n_{TOT}\right)$ values at the final steady-state were smaller than in the Half-Only condition. This is illustrated in Figure 5A. However, the difference was not significant according to the one-way repeated-measure ANOVA. There was no consistent modulation of $\Delta V_Z(F^n)$ with time in either Empty-Half or Full-Half conditions.

The time profiles of $\Delta V_Z(F^t)$ were similar across the Empty-Half and Full-Half conditions with a drop in the middle of the trial (Figure 5B). The time modulation of $\Delta V_Z(F^t)$ has been confirmed by an effect of *Time* in the two-way repeated measure ANOVA ($F_{2,14} = 36.29$; $p < 0.001$). Pair-wise comparisons confirmed significant differences between $\Delta V_Z(F^t)$ in the middle of the trial and at each of the steady-states ($p < 0.01$). Overall, the Full-Half condition showed higher values of $\Delta V_Z(F^t)$ as compared to the Empty-Half condition, main effects of *Condition-2* ($F_{1,7} = 8.75$; $p < 0.05$). At the final steady-state, the effect of *Condition-1* was significant (confirmed by a one-way repeated measure ANOVA; $F_{2,14} = 14.01$; $p < 0.05$). Pair-wise comparisons showed that $\Delta V_Z(F^t)$ in the Half-Only condition was significantly larger than in the Empty-Half conditions ($p < 0.05$).

The index of moment of force co-variation, $\Delta V_Z(M_{TOT})$ was positive at all times and showed a change with time in the Full-Half and Empty-Half conditions. Its time profiles were, however, different (Figure 5C). The index in the Empty-Half condition was significantly larger than in the Full-Half condition at the initial steady-state (PRE); then, $\Delta V_Z(M_{TOT})$ showed a drop in the Empty-Half condition and an increase in the Full-Half condition. At the final steady-state (POST), there was no significant difference among the conditions. These effects were confirmed by a main effect of *Condition-2* ($F_{1,7} = 6.12$; $p < 0.05$) and a significant *Time* × *Condition-2* ($F_{2,14} = 6.05$; $p < 0.05$) interaction in a two-way repeat measure ANOVA. Pair-wise comparisons confirmed the difference between the $\Delta V_Z(M_{TOT})$ values at the initial steady-state ($p < 0.05$).

IF Level—At the IF level, $\Delta V_Z(F^n)$ values were relatively low in all three conditions corresponding to negative ΔV values; that is, there was no synergy stabilizing F^n of VF by co-varied adjustments of the normal forces of individual fingers. In the Empty-Half condition, $\Delta V_Z(F^n)$ started with lower values and increased with time, while in the Full-Half condition the trend was opposite: $\Delta V_Z(F^n)$ dropped with time (Figure 5D). These observations were supported by a two-way repeated-measures ANOVA, which showed a significant interaction *Time* × *Condition-2* ($F_{2,14} = 11.36$; $p < 0.01$) and no other significant effects. Pair-wise comparisons confirmed that at the POST state, $\Delta V_Z(F^n)$ in the Empty-Half condition was significantly higher than in the Full-Half condition. These observations were also supported by a one-way ANOVA on the data at POST across the three conditions that showed a significant effect of *Condition-1* ($F_{2,14} = 4.05$; $p < 0.05$).

At the IF level, $\Delta V_Z(F^t)$ was positive in all three conditions and at all times. In the Empty-Half condition $\Delta V_Z(F^t)$ was larger than in the Full-Half condition. In both conditions, there was a decrease in the $\Delta V_Z(F^t)$ index during the first half of the trial and an increase in the second half of the trial (Figure 5E). The effect of *Time* was confirmed in a two-way ANOVA ($F_{2,14} = 4.92$; $p < 0.05$), and pair-wise comparisons showed that the $\Delta V_Z(F^t)$ in the middle of trial was significantly lower than at the final steady-state. At the final steady-state, there was no significant difference among the $\Delta V_Z(F^t)$ for the three conditions.

The $\Delta V_Z(M_{TOT})$ index was positive in all three conditions. There were no significant differences across the conditions and no time effects. There was no significant effect of *Condition* at the final steady-state either.

Variance Analysis

Changes in the index of co-variation (ΔV) could potentially reflect changes in either of the two variance indices that were used to compute ΔV, sum of the variances of the elemental variables, $\sum Var(EVs)$, and variance of their combined output, $Var(\sum EVs)$. We analyzed each of those two variance indices separately at both levels of the hierarchy, VF-TH and IF, and for each of the three main variables, F^n, F^t, and M_{TOT}. At the VF-TH level, the values of $[\Sigma Var(EV)]$ for all three variables were about an order of magnitude larger than the values of $[Var(\Sigma EV)]$ (compare the left panels in Figures 6 and 7). The differences were much smaller at the IF level (see the right panels in Figures 6 and 7).

Figure 6 illustrates the data for $\sum Var(EVs)$. The general trend is similar across all three variables and two levels, with the exception of F^n analysis at the VF-TH level. There is a monotonic drop in $\sum Var(EVs)$ during the Full-Half trials and a monotonic increase during the Empty-Half trials, while on average the magnitudes during the Full-Half trials were higher. These effects were confirmed by the main effects of both factors and significant interactions in the two-way repeated measures ANOVAs *Condition-2×Time* (F-values ranging from 6.2 to 13; $p < 0.05$). Pairwise contrasts with Bonferroni corrections confirmed significant differences at the PRE state between the Full-Half and Empty-Half conditions while such differences were absent at the POST state.

Figure 7 illustrates the data for $Var(\sum EVs)$. These indices were higher for the Full-Half condition as compared to the Empty-Half condition, except for F^t analyzed at the VF-TH level. No time changes were observed for the indices computed for F^n (panels A and D, Figure 7). The indices computed for M_{TOT} showed an increase during the Full-Half condition and a drop during the Empty-Half condition (panels C and F, Figure 7). A similar trend was observed for the index computed for F^t at the IF level (panel E), while at the VF-TH level this index showed an increase in the middle of the trial under both conditions (panel B, Figure 7). All the mentioned effects were statistically significant according to the two-way repeated measures ANOVAs *Condition-2×Time* (F-values ranging from 5.5 to 16; $p < 0.05$) followed by pairwise contrasts with Bonferroni corrections ($p < 0.05$). In particular, $Var(\sum EVs)$ for F^t in the middle of the trial was higher than at PRE and POST under both Full-Half and Empty-Half condition ($p < 0.05$)

There were no differences in any of the mentioned indices across the three conditions at the POST state. Correspondingly, no significant effects of *Condition-1* were observed in the one-way repeated measures ANOVA.

Discussion

A number of the current findings show that, when a person holds a half-filled container, characteristics of the action and indices of digit interaction partly depend on whether the container has just been filled (half-full), emptied (half-empty), or stayed half-filled throughout the trial. To our knowledge, such history effects have not been reported earlier. In our experiments, such effects were seen in averaged across trials characteristics, such as local safety margin, as well as in co-varied adjustments of digit forces across trials. Further we discuss relations between these observations and current views on the organization of human static prehension.

Balancing an inverted pendulum

The task of holding the handle with the container in our experiment may be viewed as balancing an inverted pendulum. Such tasks have been commonly considered in the area of the control of vertical posture (Winter et al. 1996; Creath et al. 2005) as well as for tasks of balancing an inverted pendulum using the hand (Lakie and Loram 2006; Loram et al. 2006; Foo et al. 2000; Gawthorpe et al. 2009; Cluff and Balasubramaniam 2009; Milton et al. 2009b). The group of Lakie and Loram studied the control of an inverted pendulum via a spring-like linkage and found that the balancing process was always characterized by repeated small reciprocating hand movements. These adjustments were interpreted as a sign of predictive intermittent alterations in neural output. Milton and colleagues suggested that balancing a stick on the fingertip is associated with a "drift and act" mechanism, which involves accumulation of an error signal associated with deviation of the stick from the vertical until a threshold value is exceeded, followed by a corrective action.

Our task was different from balancing a pole: Pole balancing requires kinematic control of the supporting surface, while in our task the container was secured to the platform held by the subjects such that the subjects always kept the object and the hand nearly motionless, and had to apply moments of force to the handle to keep the object vertical. It is common knowledge that balancing a very light object (for example, a plastic straw) on the fingertip is harder than balancing a heavier object with a higher center of mass location (for example, a billiard cue stick). This may be related to three aspects. First, higher COM location and larger moment of inertia afford more time for correction when the pole starts to deviate from the vertical. Second, somatosensory receptors provide better resolution for heavier objects as compared to very light ones. Third, physiological tremor induces larger deviations of a light object as compared to a heavier one. Note that similar conclusions and arguments have been presented in a series of studies of angular stick fluctuations with respect to the vertical during balancing the stick on the fingertip (Cabrera and Milton 2004 Milton et al. 2009a,b). They are compatible with the mentioned "drift and act" mechanism proposed by Milton and colleagues (2009b).

In our experiment, the empty condition was associated with the lowest COM location, and the full condition corresponded to the highest COM location. Hence, we view the Empty-Half condition as the one starting from the most challenging Empty state (cf. Cabrera and Milton 2004; Milton et al. 2009b) where the word "challenging" implies permissible errors in total moment of force magnitude. In contrast, the Full-Half condition starts from the least challenging Full state. This may be the reason for the different behaviors of the synergy index computed for the total moment of force applied to the handle ($\Delta V(M_{TOT})$, Figure 5C). In the most challenging state (Empty), the subjects showed the highest values of this index related to stabilization of the moment of force. This index dropped as the container was filled. In the Full-Half condition, the trend was opposite, the $\Delta V(M_{TOT})$ index started from a lower value and increased over time. Note that this explanation is oversimplified; in particular, it does not consider possible water waves in the container.

Overall, these results support earlier observations in experiments with moving objects of different fragility (Gorniak et al. 2010). That study also compared more and less challenging tasks with respect to constraints on the permissible normal force magnitude, not on the total moment of force as in the current study. Gorniak and colleagues have found that making a task more challenging leads to higher indices of synergies stabilizing salient mechanical variables. Higher synergy indices computed with respect to the normal force applied by the virtual finger (at the IF level) were observed in the study of Gorniak et al. (2010) when the subjects moved more fragile objects. Similarly, in the current study this index increased over the Empty-Half trials while it decreased over the Full-Half trials.

Another relevant result is the consistent changes in the moment of force magnitudes produced by the thumb and VF with the weight of the object. The thumb and VF produced non-zero moments of force directed against each other such that the total moment of force was always very close to zero, as required by the task (see also Zatsiorsky et al. 2002). The notion of co-contraction is commonly used in motor control literature referring to simultaneous activation of muscles with opposing actions (an agonist-antagonist pair) resulting in a zero net torque effect on the joint spanned by the muscles. Muscle co-contractions are commonly interpreted as the means of increasing the apparent stiffness of the joint (Latash and Zatsiorsky 1993) to stabilize it against possible perturbations (Woollacott et al. 1988; Bouisset and Zattara 1990; McIntyre et al. 1996). The opposing digits, the thumb and VF, in our experiment played the role of "muscles" producing moments of force on the handle in opposite directions. An increase in the magnitude of those moments of force may be viewed as a "moment co-contraction", possibly with the same purpose – that is, to increase stability of the object in conditions of its larger weight and higher location of the center of mass. A mechanism to produce the observed pattern of changes in the moments of force may involve proportional scaling of digit forces with the weight of the hand-held object without changes in the force sharing pattern. Such proportional scaling strategy fits earlier observations of digit force adjustment to changes in load without changes in the external torque (Zatsiorsky et al. 2002).

Interactions between synergies at different hierarchical levels

As in several earlier studies, we assumed that the control of the hand action was based on an hierarchy with two levels (Arbib et al. 1985). At the upper level (VF-TH), the task was shared between the thumb and VF, while at the lower level, action of the VF was shared among the four fingers of the hand. Based on several earlier studies (Gorniak et al. 2007a,b, 2009a,b), we expected to see signs of a trade-off between synergies stabilizing mechanical variables at the two levels of the assumed hierarchy. Note that the method of computing synergy indices favors such a trade-off: Indeed, a highly positive synergy index at the higher level implies large amount of "good" variance, V_{GOOD}. Since V_{GOOD} contributes to the variance of each elemental variable, this means that variance of VF is correspondingly high. However, at the lower level of the hierarchy variance of VF is by definition V_{BAD}, and this favors low synergy indices at the IF level. As shown in an earlier study (Gorniak et al. 2009b), this trade-off is not absolute, and the central nervous system can overcome it.

Several of the observations support the prediction about the trade-off between synergies at the VF-TH and IF levels. In particular, there were highly positive synergy indices for the normal force at the VF-TH level, while at the IF level values of these indices were mostly negative corresponding to lack of a synergy stabilizing the VF normal force by co-varying adjustments of finger normal forces. This observation is similar to those made in an earlier study by Gorniak et al. (2009b).

A more subtle example of the trade-off was observed for the synergy indices computed with respect to tangential force. At both levels, the $\Delta V(F^t)$ indices were positive indicating synergies stabilizing both VF tangential force and total tangential force (cf. Gorniak et al. 2009b). However, indices of synergies stabilizing tangential (load-resisting) force were higher for the Full-Half condition compared to the Empty-Half condition when quantified at the TH-VF level. In contrast, at the IF level, these indices were higher for the Empty-Half condition.

We found no clear proof of a trade-off between the two levels for the synergy indices computed for the moment of force. At both levels, the indices were positive. There were significant time trends of those indices at the VF-TH level and also the indices were higher for the Empty-Half condition. However, no significant differences were found at the IF level.

When the two main variance indices, ∑Var(EVs) and Var(∑EVs), were analyzed separately, it became clear that most non-trivial findings resulted from the behavior of the latter index, analogous to V_{BAD} or non-goal-equivalent variance (NGEV, Scholz et al. 2007) within the framework of the UCM hypothesis. In particular, the non-monotonic behavior of ΔV computed for F^t reflected primarily the non-monotonic behavior of Var(∑EVs). Most of the other variance indices showed a drop during the Full-Half trials and an increase during the Empty-Half trials. For F^n and F^t, these trends may be viewed as straightforward reflections of the well-known scaling of force variance with force magnitude (Newell and Carlton 1988; Slifkin and Newell 1999; Christou et al. 2002), a reflection of a signal-dependent noise (Harris and Wolpert 1998). Indeed, both F^n and F^t dropped during the Full-Half trials and increased during the Empty-Half trials. However, similar patterns were observed for the indices computed for M_{TOT}, while the total moment of force was close to zero at all times. These results likely reflected the scaling of the forces contributing to M_{TOT} over the trials (see, for example, Zatsiorsky et al. 2002) leading to a nearly proportional scaling of their variances. The negative co-variation of the moments produced by tangential and normal forces kept M_{TOT} low.

Time and history effects on prehension synergies

While most outcome variables showed smooth unidirectional time changes in the Empty-Half and Full-Half conditions, two indices showed a transient decrease in the middle of the trial, while the values at the initial (PRE) and final (POST) steady-states were similar. Those are the synergy indices computed with respect to tangential force at both levels of the hierarchy (the middle panels in Figure 5). Transient drops in synergy indices have been reported during tasks with changes in the respective mechanical variables (Latash et al. 2002a; Friedman et al. 2009; SKM et al. 2010). Such patterns have been interpreted within the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999), which quantifies two components of variance, “good variance” (V_{GOOD}) that does not affect a particular performance variable, and “bad variance” (V_{BAD}) that does.

Several studies of multi-finger force production have shown that V_{GOOD} increases with the force magnitude, while V_{BAD} increases with the magnitude of force rate, dF/dt (Latash et al. 2002a; Friedman et al. 2009; SKM et al. 2010). The latter effect has been linked to timing errors across trials (Goodman et al. 2005). The profiles of ΔV(F^t) in our study qualitatively fit this explanation. However, the peak rate of F^t in the current experiment was extremely low, about 0.5 N/s, while in the cited earlier studies the peak force rate was at least 100 times higher. So, either we are dealing with an exceptional sensitivity of ΔV(F^t) to timing errors, or there is a different reason for the non-monotonic ΔV(F^t) time profiles. There are two arguments supporting the latter suggestion. First, the rate of force change was nearly constant over the trial duration while ΔV(F^t) showed a clear trough in the second portion of the trial. Second, no such effects were observed for the synergy index for normal force, ΔV(F^n) while the time profile of the normal force was similar to that of the tangential force

(Figure 2). The apparent similarity of the patterns for the normal and tangential forces in Figure 2 contrasted by the clear difference between the corresponding synergy indices (Figure 5) remains unexplained. It suggests that that rate of change of the performance variable is only one factor that defines synergy indices.

Significant history effects for the data at the POST state were found for the safety margin and for several synergy indices. The overall pattern of differences across the three conditions was similar for the SM_{TH} and the index of synergy computed with respect to the total tangential force at the TH-VF level, $\Delta V(F^t)$. For both indices, the pattern was Half-Only > Full-Half > Empty-Half (Figures 4 and 5B), although not all the inequalities reached statistical significance. The lower SM_{TH} for the tasks associated with a change in the total tangential force is not completely unexpected. A few earlier studies with moving hand-held objects (Zatsiorsky et al. 2005) and with applying tangential forces in isometric conditions (Jaric et al. 2005) documented lower safety margin values for tasks performed at higher frequencies. Note, however, that, in contrast to the cited studies, in our experiment the measurements were performed at steady-states, and the load changes were very slow. So, effects of changing total tangential force persist at very slow changes and outlast the actual time of such changes.

Using relatively low $\Delta V(F^t)$ for the Full-Half and Empty-Half tasks may be interpreted as the subjects preferring to perform those tasks with overall lower stability. This interpretation makes the current findings of lower ΔV indices similar to the phenomena of anticipatory synergy adjustments (ASAs), that is a drop in a synergy index in anticipation of a quick change of the performance variable (Olafsdottir et al. 2005; Shim et al. 2005). The purpose of ASAs has been assumed to avoid fighting one's own synergy when a quick change in the performance variable is needed (see also Kim et al. 2006). When the weight of the object in one's hand changes, this by itself requires a slow change in the total tangetial force. Even after the load changes stopped, the subject's central nervous system may still be expecting possible load changes reflected in the lower synergy index for F^t. This conclusion seems to contradict the results of an earlier study (de Freitas et al. 2007) with the task to reach quickly towards a certain or uncertain target. The results showed a significant increase in the goal-equivalent variance (analogous to our V_{GOOD}) in the uncertain target condition resulting in higher indices of a kinematic synergy stabilizing the endpoint trajectory. A major difference between the de Freitas et al. study and the current study is that the task in our study was predictable and nearly steady-state, unlike the target jumps during the quick reaching movement in the de Freitas study. So, in the de Freitas et al. study, an ability to change the action quickly was crucial for success while in our study this was not the case. Still, we admit that our current conclusion remains tentative and requires further investigation.

The steady holding task in our study allowed for some minor motion of the handle and changes in its orientation. Indeed, the subjects used an air bubble level to keep the handle vertical. They could produce deviations of the handle from the vertical on the order of 2° (the tolerance of the level). Such deviations could theoretically affect the computed synergy indices. We view such effects as unlikely because they would imply that all the subjects reacted to different conditions by tilting the handle reproducibly in the same way within the tolerance margin.

To summarize, we presented evidence for history dependence of indices of digit coordination during steady holding of an object secured to the handle. The results obviously cannot be generalized beyond the studied experimental conditions, in particular to manipulation of such objects and balancing objects not secured to the handle. While physiological interpretation of the results is tentative and incomplete, the observations show that the human central nervous system distinguished between half-full and half-empty glasses at the level of digit coordination.

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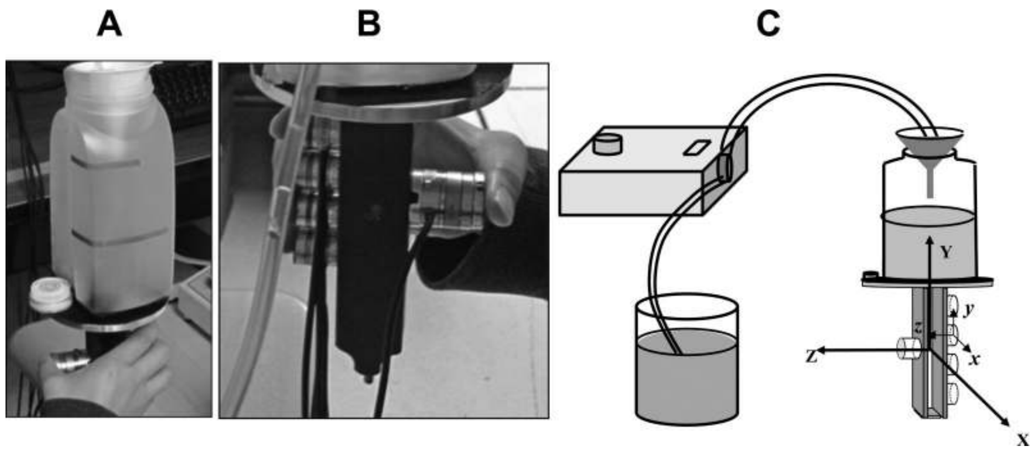

Figure 1.
The experimental setup. A: The handle with the container on top. B: The digit positions on the force sensors. C: The schematics of the setup and the main coordinate systems.

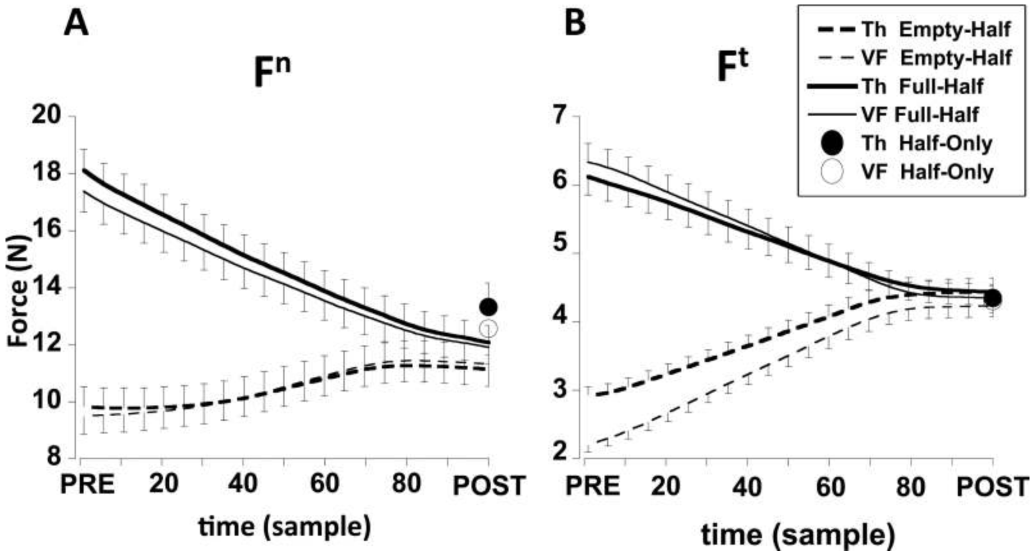

Figure 2.

Changes in the normal forces (F^n, panel A) and tangential forces (F^t, panel B) of the thumb (TH) and virtual finger (VF). Averaged across subjects data are shown with standard error bars plotted for every fifth time sample. The time scale shows the two steady-states (PRE and POST) and the 100 re-sampled points during the transition period. The solid lines show the data for the Full-Half condition, and the dashed lines show the data for the Empty-Half condition. The data for the Half-Only condition are shown with large symbols aligned with the POST time sample.

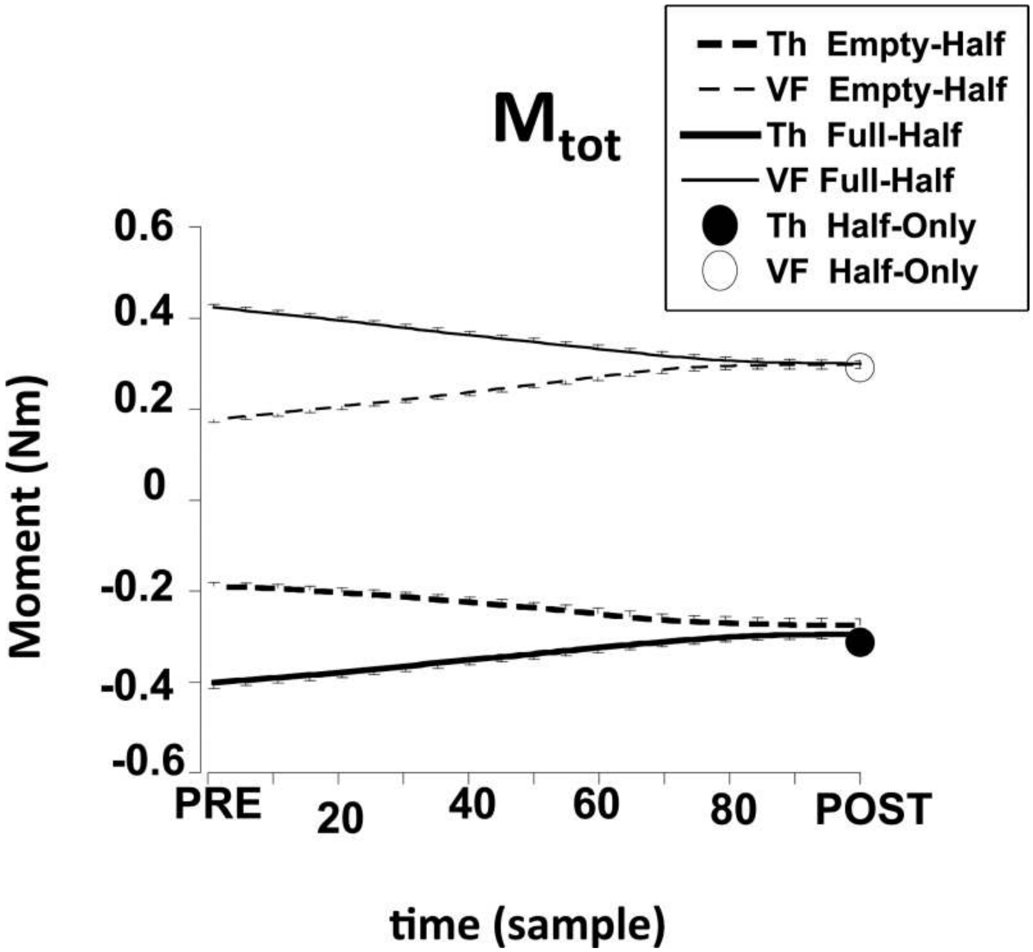

Figure 3.

Changes in the moment of forces (*M*) produced by the thumb (TH) and virtual finger (VF). Averaged across subjects data are shown with standard error bars plotted for every fifth time sample. The time scale shows the two steady-states (PRE and POST) and each of the 100 re-sampled points. The solid lines show the data for the Full-Half condition, and the dashed lines show the data for the Empty-Half condition. The data for the Half-Only condition are shown with large symbols aligned with the POST time sample.

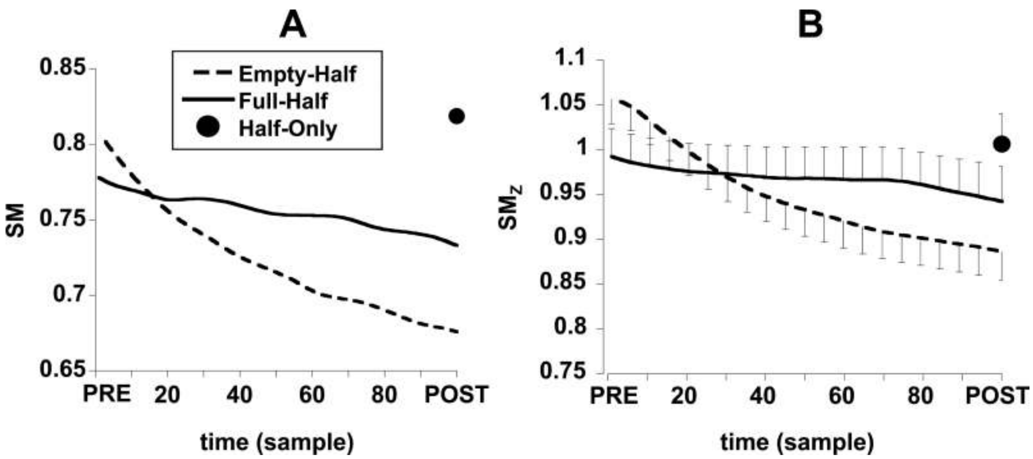

Figure 4.

Changes in the safety margin (SM) for a representative subject (panel A), and changed in the z-transformed SM values (SM_Z) averaged across subjects with standard error bars plotted for every fifth time sample. The time scale shows the two steady-states (PRE and POST) and each of the 100 re-sampled points. The solid lines show the data for the Full-Half condition, and the dashed lines show the data for the Empty-Half condition. The data for the Half-Only condition are shown with large symbols aligned with the POST time sample.

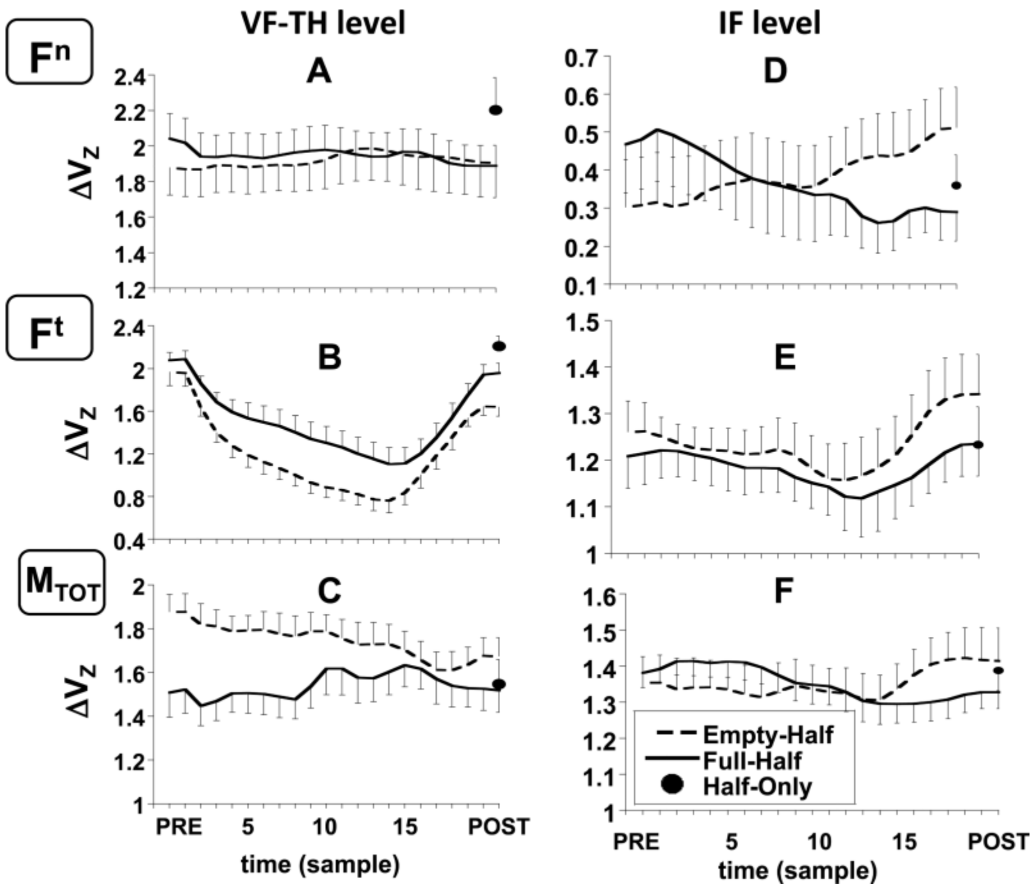

Figure 5.
Indices of co-variation of elemental variables computed at the two levels of the assumed hierarchy, the VF-TH level (left panels) and the IF level (right panels). The indices were z-transformed (ΔV_Z) and averaged across subjects; standard error bars are shown. The top panels (A and D) show ΔV_Z indices for the normal forces, the middle panels (B and E) – for the tangential forces, and the bottom panels (C and F) – for the moments of force. The time scale shows the two steady-states (PRE and POST) and each of the 20 re-sampled points. The solid lines show the data for the Full-Half condition, and the dashed lines show the data for the Empty-Half condition. The data for the Half-Only condition are shown with large symbols aligned with the POST time sample.

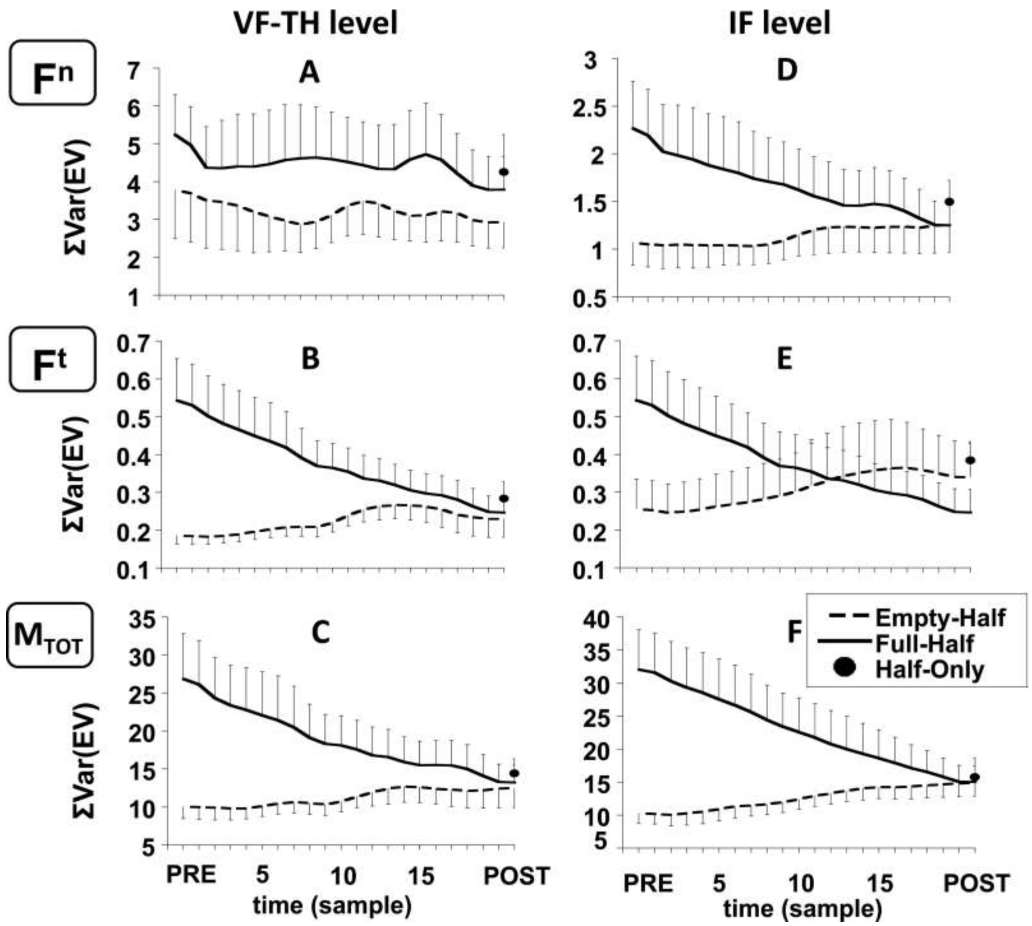

Figure 6.

Sum of the variances of the elemental variables, ∑Var(EVs), computed at the two levels of the assumed hierarchy, the VF-TH level (left panels) and the IF level (right panels) with standard error bars. The top panels (A and D) show the indices for the normal forces, the middle panels (B and E) – for the tangential forces, and the bottom panels (C and F) – for the moments of force. The time scale shows the two steady-states (PRE and POST) and each of the 20 re-sampled points. The solid lines show the data for the Full-Half condition, and the dashed lines show the data for the Empty-Half condition. The data for the Half-Only condition are shown with large symbols aligned with the POST time sample.

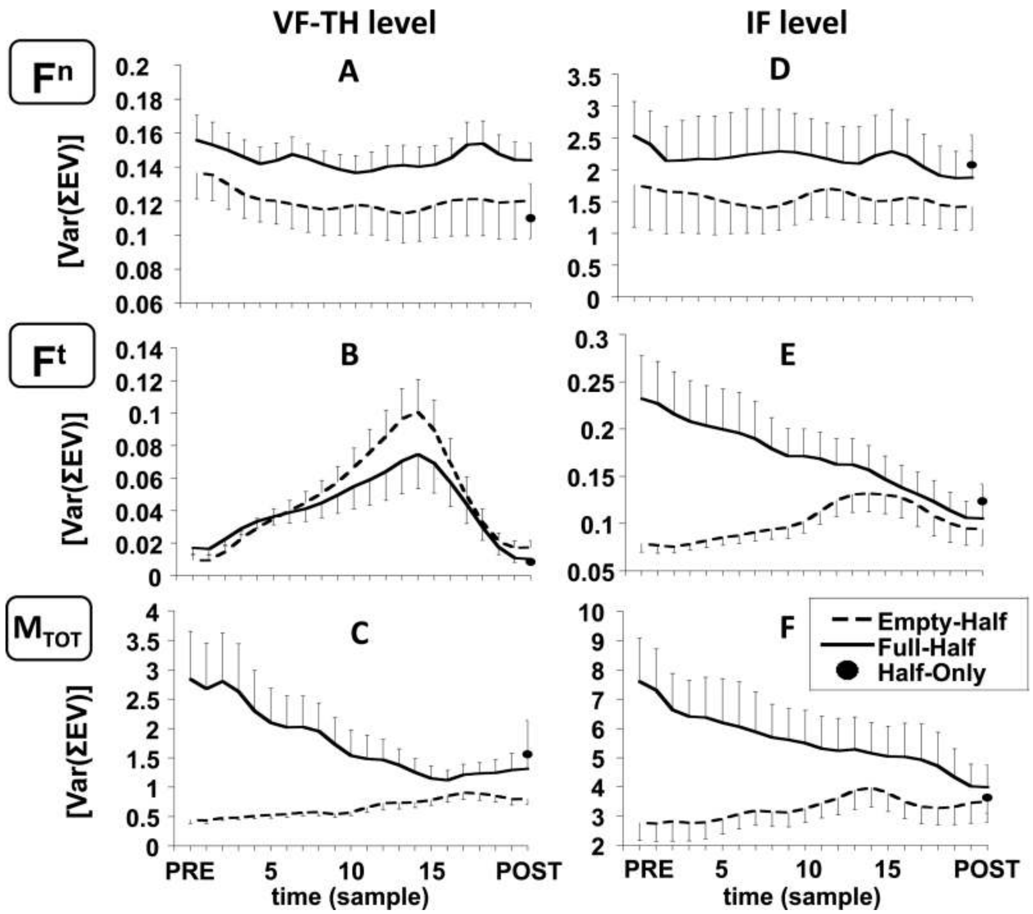

Figure 7.

Variance of the combined output of the elemental variables, Var(∑EVs), computed at the two levels of the assumed hierarchy, the VF-TH level (left panels) and the IF level (right panels) with standard error bars. The top panels (A and D) show the indices for the normal forces, the middle panels (B and E) – for the tangential forces, and the bottom panels (C and F) – for the moments of force. The time scale shows the two steady-states (PRE and POST) and each of the 20 re-sampled points. The solid lines show the data for the Full-Half condition, and the dashed lines show the data for the Empty-Half condition. The data for the Half-Only condition are shown with large symbols aligned with the POST time sample.