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RESEARCH ARTICLE

Prehension synergies during smooth changes of the external torque

Yao Sun · Jaebum Park · Vladimir M. Zatsiorsky · Mark L. Latash

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Abstract We studied characteristics of digit action and their co-variation patterns across trials (prehension synergies) during static holding of an object while the external torque could change slowly and smoothly. The subjects held in the air an instrumented handle with an attachment that allowed a smooth change in the external torque over about 12 s; the load was always kept constant. Series of trials were performed under three conditions: The torque could be zero throughout the trial, or it could change slowly requiring a smooth change of the effort from a non-zero pronation value to zero (PR-0) or from a non-zero supination value to zero (SU-0). The handle was kept vertical at all times. Indices of variance and co-variation of elemental variables (forces and moments of force produced by individual digits) stabilizing such performance variables as total normal force, total tangential 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, the action of the virtual finger is shared among the actual four fingers. We analyzed the total moment of force as the sum of the moments of force produced by the thumb and virtual finger and also as the sum of the moments of force produced by the normal forces and tangential forces. The results showed that the adjustments in the total moment of force were produced primarily with changes in the moment produced by the virtual finger and by changes in the moment produced by the normal forces. The normal force of the thumb at the final state (which was the same across conditions) was larger in the two conditions with changes in the external torque. The safety margin was significantly higher in the PR-0 condition, and it dropped with the decrease in the external torque. A co-contraction index was computed to reflect the moment of force production by the fingers acting against the total moment produced by the virtual finger. It was higher for the SU-0 condition. Most variance indices dropped with a decrease in the external torque. The co-variation indices, however, remained unchanged over the trial duration. They showed signs of a trade-off between the two levels of the assumed hierarchy: larger indices at the higher level corresponded to smaller indices at the lower level. This study and the previous one (Sun et al. in Exp Brain Res 209:571–585, 2011) document several previously unknown features of prehensile tasks. The results show that characteristics of digit action and interaction in such tasks depend not only on the magnitudes of external constraints but also on a variety of other factors including time changes in the constraints and their history.

Keywords Prehension · Safety margin · Synergy · History effects

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Introduction

When a person holds steadily an object with all five digits using a prismatic grasp (the thumb opposing the four fingers), the number of constraints imposed by the task is smaller than the number of kinetic variables the digits produce (Zatsiorsky and Latash 2004). This leads to the problems of motor redundancy (Bernstein 1967), which have been analyzed at two levels of a hypothetical hierarchy involved in the control of prehensile actions (Arbib et al. 1985). At the upper level (VF–TH level), the task is shared between the actions of the thumb and a virtual finger (VF), an imaginary digit with mechanical action equal to that of the four fingers combined. At the lower level (IF level), the VF action is shared among the fingers. The notion of prehension synergies has been used to address co-varied changes in elemental kinetic variables (such as forces and moments of force produced by individual digits) produced by digits at a given level of analysis that stabilizes an output produced by all the digits combined (such as the total force and moment of force vectors; reviewed in Latash et al. 2007; Zatsiorsky and Latash 2008; Latash and Zatsiorsky 2009). A synergy at the VF–TH level assumes that elemental variables produced by the thumb and VF co-vary across trials to satisfy task mechanics, whereas a synergy at the IF level means that elemental variables produced by fingers co-vary to ensure low variance of the VF output.

Most earlier studies analyzed synergies during static prehensile tasks with no changes in the external load and torque magnitudes (for a notable exception, see Friedman et al. 2009). In a recent study, history effects have been documented on indices of multi-digit synergies at both levels of the introduced hierarchy when the subjects reached the same magnitude of external load starting from different initial load values (Sun et al. 2011). These observations extended the list of neuromuscular phenomena that show effects of hysteresis (Partridge 1965; Gielen et al. 1984; Kostyukov 1998) to patterns of digit co-variation.

The study of Sun et al. (2011) used slow changes in the weight of a hand-held “glass” by either filling it to the half from an empty state or emptying it to the half from a full state. The external torque was always very small and did not change consistently during the trials. In the current study, we continue to explore effects of history and time-varying external constraints on digit interaction using a comparably slow change in the external torque while the load is kept constant. Based on earlier observations, we formulated the following four hypotheses.

First, we expected the normal forces produced by the thumb and VF to be smaller in conditions involving changes in the torque to a certain final value as compared to a condition when the same torque value was presented from the beginning of the trial (Sun et al. 2011). Since the load is always constant, this implies an increase in the safety margin (proportion of the normal force above the threshold for slippage, Johansson and Westling 1984) in conditions with changes in the external torque. Second, the external torque had to be balanced by the moment of force produced by the subjects. Based on earlier studies (Zatsiorsky et al. 2002, 2003), we expected the total moment of force to be shared nearly equally between the moments produced by the normal forces and moments produced by the tangential forces across all levels of the external torque. Third, an earlier study (Gorniak et al. 2009) documented a trade-off between synergy indices at the two levels of the hierarchy, that is stronger synergy indices at the VF–TH level were associated with smaller synergy indices at the IF level. Therefore, we expected to see a similar trade-off in this experiment. Fourth, non-monotonic changes in synergy indices were expected in trials involving a change in the external torque magnitude with a drop in the indices in the middle of the trial (Latash et al. 2002a; Goodman et al. 2005; Sun et al. 2011).

The framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999; reviewed in Latash et al. 2002b, 2007) was used to quantify multi-digit synergies. The UCM hypothesis views motor tasks as being performed within a space of elemental variables (such as 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 (such as resultant force and/or 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 (ΔV) reflecting the relative amount of V_{GOOD}.

To test the hypotheses, we quantified variance indices computed across repetitive trials at comparable phases at the two levels of the hierarchy separately (VF–TH and IF), sharing of the total torque between the moments produced by the normal and tangential forces, and the safety margin values in trials with and without changes in the external torque.

Methods

Participants

Eight male subjects participated in this study. On average, they were 26 ± 4 years of age, 1.86 ± 0.06 m in height, 72.64 ± 9.75 kg in mass, 0.0825 ± 0.0065 m in right-hand width and 0.1938 ± 0.0048 m 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 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 for Regulatory Compliance of the Pennsylvania State University.

Experimental setup

Five-six-component force–moment transducers (Nano-17 for each digit; ATI Industrial Automation, Garner, NC, USA) were mounted on a handle made of aluminum (Fig. 1, panels a, b, c). The center points of the sensors for the index and middle fingers were 0.045 and 0.015 m above the midpoint of the handle, respectively. The center points of the sensors for the ring and little fingers were 0.015 and 0.045 m below the midpoint of the handle, respectively. The thumb sensor was located at the midpoint of the handle. The horizontal distance between the sensor surfaces was 0.06 m. The centers of all the sensors were within one plane referred to as the grasp plane.

An aluminum beam, 0.52 m in length and 0.05 m in height, was fixed at the bottom of the handle horizontally with the handle aligned with the center of the beam. A 24V DC/5,500 rpm TRW Globe Motor (Globe Motors, Dayton, OH, USA) was fixed at the center of the beam. The motor could move a 0.15-kg load smoothly with a speed of about 0.02 m/s along the beam using a thread-and-pulley system (Fig. 1, panels a, c). There was a stop in the middle of the beam; as soon as the load touched the stop, an experimenter turned the motor off. The load could move over 0.24 m from one end of the beam to its center, and the maximal external torque at the extreme load positions was about 0.35 Nm.

The total mass of the handle with five sensors, the aluminum beam, and the motor was 0.95 kg. Sandpaper (100-grit) was attached to the contact surface of each sensor to increase the friction between the digits and the transducers. Similar to earlier studies (Shim et al. 2003, 2004a, b; Gorniak et al. 2009), 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. A circular level with 2° tolerance was attached on the top of the handle and used as a feedback device for the subject to keep the handle orientation vertical at all times.

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,

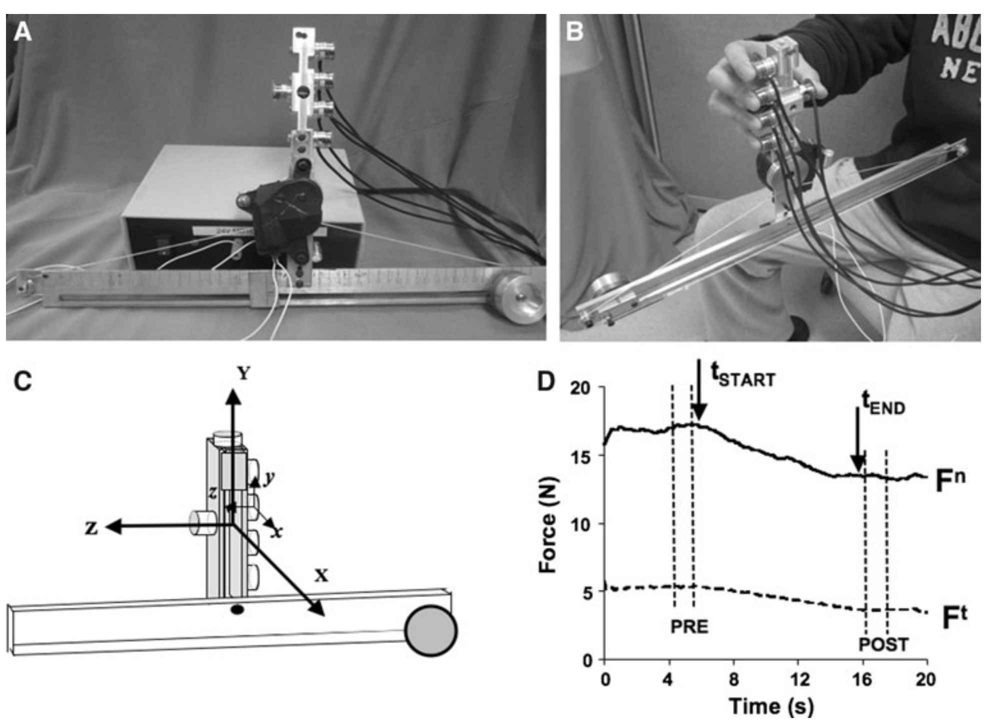

Fig. 1 The experimental setup. **a** The handle and motor. **b** The digit positions on the sensors. **c** The schematics of the setup and the main coordinate systems. **d** A typical single trial in the PR-0 condition (the subject produced pronation effort against the external torque). The time profiles of the normal force (F^n) and tangential force (F^t) of the virtual finger are shown. The time intervals for the assessment of the PRE and POST states are shown with *vertical dashed lines*; these were defined as the 0.5-s time interval starting 0.5 s away from the start and the end of the transient state. The times of load motion initiation and termination are shown with *arrows*

TX, USA). A customized LabView program (National Instruments, Austin, TX, USA) was used for data sampling at 100 Hz, and a customized MATLAB program (Mathworks Inc., Natick, MA, USA) was written for data processing.

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 (Fig. 1b). When holding the handle, the subject's right upper arm was abducted at approximately 45° in the frontal plane and internally rotated approximately 30°, the elbow was flexed approximately 90°, and the wrist 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 0.25 m.

There were three conditions in this study where the external load could be: (1) originally placed at the end of the beam closer to the torso of the subject, which required the subject to produce a supination effort and then moved by the motor to the center of the beam (SU-0); (2) originally placed at the other end of the beam (the end away from the torso of the subject), which required the subject to produce a pronation effort and then moved by the motor to the center of the beam (PR-0); and (3) kept at the center of the beam (0-Only). 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 statically without deviations from the vertical (keeping the air bubble in the center of the level) until the experimenter informed that the trial was over. The duration of each trial was 10 s in the 0-Only condition and 20 s in the SU-0 and PR-0 conditions. In the SU-0 and PR-0 conditions, the subject held the handle steadily for the first 3–4 s, and then the experimenter turned on the motor to start the load motion toward the center of the beam. Once the load reached the center of the bar, the experimenter turned the motor off, while the subject continued to hold the handle statically and vertically for 3–4 s until the end of trial. The central location of the load was clearly marked, and a stop prevented the load from moving beyond the central location. The subjects looked at the level at all times. After each trial, the experimenter moved the load to its initial position. Subjects were allowed to take a rest after each trial and between conditions to avoid fatigue. The intervals after each trial were about 30 s, and the intervals between conditions were about 5 min. The first four subjects performed 15 consecutive trials in each condition (45 trials in total). The last four subjects performed 20 trials under each condition (60 trials in total). The order of the conditions was randomized.

Data processing

Further, we use "external torque" to describe the moment produced by the gravity force acting on the external load with respect to the horizontal axis orthogonal to the plane of the grasp (the plane containing the centers of all the digit sensors) and passing through the geometric center of the handle. "Moment of force" (sometimes, "moment" for brevity) is used to describe the moments produced by forces generated by the subject (by the hand, by particular forces, or by individual digits).

Data were low-pass filtered at 10 Hz using a fourth-order, zero-lag Butterworth filter. Before further processing, total normal force, total tangential force, and total moment of force produced by the thumb and virtual finger were calculated for each trial to check whether the laws of statics were satisfied. In particular, we checked that $F^n_{TOT} = F^n_{VF} + F^n_{TH} = 0$; $F^t_{TOT} = F^t_{VF} + F^t_{TH} = -W$; and $M_{VF} + M_{TH} = 0$ (only for the central position of the load). In these equations, the superscripts stand for the normal and tangential forces (n and t, respectively), while the subscripts stand for the variables produced by the virtual finger (VF) and the thumb (TH); W stands for the weight of the system, F stands for force and M stands for moment of force, subscript TOT stands for "total." If any of the mentioned constraints were violated by more than two standard deviations computed for each of the variables produced by the digits (VF and TH) over trials, that trial was deleted. The total number of accepted trials across all subjects was 375 (out of 420).

For each trial in the SU-0 and PR-0 conditions, the total moment of force produced by all five digits, $M_{TOT,}$ with respect to the geometrical center of the handle was computed. First, the time intervals 1.5–2.5 and 16–17 s were taken as steady-states, that is before any load motion could happen and after the motion was completed in all trials. The mean total moment of force, M_{TOT}, and its standard deviation were computed over the samples within each steady-state. The time of load movement initiation (t_{START}) was defined as the time when M_{TOT} deviated from its mean value during the first steady-state interval by more than two standard deviations. The time of load movement termination (t_{END}) was defined using the same criterion with respect to the second steady-state interval (Fig. 1d). The data between t_{START} and t_{END} were re-sampled to 100 points. For each dependent variable, the data were also averaged over the 0.5-s time intervals starting 0.5 s away from t_{START} to t_{END}, respectively, and the averaged values were used to represent the initial steady-state (PRE) and final steady-state (POST) (Fig. 1d). As a result, 102 values

(100 re-sampled points plus averaged values of PRE and POST) were obtained for each variable within each trial. For the 0-Only condition, the data from 3 to 5 s were averaged.

Digit forces and moments of force were computed within sensor-based reference frames for individual sensors with the axes 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 forces were computed within the handle-based reference frame (X, Y, Z) fixed at the geometric center of the handle, X, Y, $Z = 0$ (Fig. 1c). The moments of force were computed with respect to a horizontal axis orthogonal to the plane of grasp, i.e., axis X of the reference system (X, Y, Z). To compute the moment of force in the handle-based reference frame, the center of pressure coordinates for each sensor, COP, was computed using the equations for the point of wrench application (Zatsiorsky 2002):

$$\mathrm{COP}_y = M_x / F_z.$$

The moment of normal force is the moment generated by the forces acting along the Z-axis of all the digits. It was defined as:

$$M^n = M^n_{\mathrm{VF}} + M^n_{\mathrm{TH}} \quad (1)$$

$$M^n_{\mathrm{VF}} = M^n_{\mathrm{i}} + M^n_{\mathrm{m}} + M^n_{\mathrm{r}} + M^n_{\mathrm{l}} \quad (2)$$

The moment of tangential force is the moment generated by the forces acting along the Y-axis of all the digits. It was defined as:

$$M^t = M^t_{\mathrm{VF}} + M^t_{\mathrm{TH}} \quad (3)$$

$$M^t_{\mathrm{VF}} = M^t_{\mathrm{i}} + M^t_{\mathrm{m}} + M^t_{\mathrm{r}} + M^t_{\mathrm{l}} \quad (4)$$

The slip safety margin (SM, the amount of grip force exerted beyond what is required to prevent object slip; Johansson and Westling 1984; Burstedt et al. 1999; Pataky et al. 2004) for the thumb was computed as:

$$\mathrm{SM} = \frac{\left(F^n_{TH} - \left|F^t_{TH}\right|/\mu\right)}{F^n_{\mathrm{TH}}} \quad (5)$$

where μ is the coefficient of static friction between the finger pad and sandpaper interface. Since the thumb normal force equaled the VF normal force (see below), the thumb normal force was used 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. Based on earlier studies (Zatsiorsky et al. 2002; Savescu et al. 2008), we assumed $\mu = 1.4$.

The co-contraction index (CCI) was computed as

$$\mathrm{CCI} = 1 - \frac{(|M_{\mathrm{AGO}}| - |M_{\mathrm{ANT}}|)}{(|M_{\mathrm{AGO}}| + |M_{\mathrm{ANT}}|)} = 2 \times \frac{|M_{\mathrm{ANT}}|}{|M_{\mathrm{AGO}}| + |M_{\mathrm{ANT}}|} \quad (6)$$

where M_{AGO} is the total agonist moment and M_{ANT} is the total antagonist moment. In the PR-0 and SU-0 conditions, M_{AGO} was defined as the total moment of force produced by the fingers that acted in the direction of the total moment of force produced by the VF. M_{ANT} was defined as the total moment produced by the fingers that acted in the opposite direction. Note that some fingers changed the direction of their moment of force in the middle of the trial (see "Results"). In such cases, their moment of force was added to M_{AGO} or M_{ANT} at different time samples. Also note that the total moment of force produced by the VF could be directed not against the external torque but in the direction of the external torque; in such cases, the moment of force produced by the thumb made sure that the total moment of force was opposite and equal in magnitude to the external torque. Overall, the VF can generate moments of force either against or in the same direction as the external torque, while the individual fingers can generate the moments either in the same direction as the VF moment (M_{AGO}) or opposite to it (M_{ANT}).

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). At the VF–TH level, the outputs of the VF and thumb are viewed as elemental variables that produce mechanical action on the handle. At the IF level, the outputs of each individual finger within the VF are elemental variables that produce the output of the VF. So, at the IF level, the elemental variables included the normal and tangential forces of individual fingers (F^n_{j} and F^t_{j}; j = i, m, r, and l) and the moments produced by the fingers (M_j). At the VF–TH level, the elemental variables were F^n_{VF}, F^n_{TH}, F^t_{VF}, F^t_{TH}, M_{VF}, and M_{TH}.

The indices of co-variation of elemental variables were computed at each of the two levels, VF–TH and IF, for each sample across all the accepted 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 [$\sum \mathrm{Var(EV)}$] and the variance of the total output of these elemental variables [$\mathrm{Var}(\sum \mathrm{EV})$] normalized by $\sum \mathrm{Var(EV)}$ to allow comparisons across conditions and subjects:

$$\Delta V = \frac{\sum \mathrm{Var(EV)} - \mathrm{Var}(\sum \mathrm{EV})}{\sum \mathrm{Var(EV)}} \quad (7)$$

Specifically, six indices were computed:

$$\Delta V(i_{\mathrm{VF-TH}}) = \frac{\mathrm{Var}(i_{\mathrm{VF}}) + \mathrm{Var}(i_{\mathrm{TH}}) - Var(i_{\mathrm{TOT}})}{\mathrm{Var}(i_{\mathrm{VF}}) + \mathrm{Var}(i_{\mathrm{TH}})} \quad (8)$$

$$\Delta V(i_{\mathrm{IF}}) = \frac{\sum \mathrm{Var}(i_j) - \mathrm{Var}(i_{\mathrm{VF}})}{\sum \mathrm{Var}(i_j)} \quad (9)$$

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 (Eq. 8) or by the individual fingers (Eq. 9). We interpret $\Delta V > 0$ as sign of a force (or moment of force) stabilizing synergy (Shim et al. 2005; Gorniak et al. 2009). Large positive ΔV values correspond to larger amounts of negative co-variation, thus a stronger synergy. A result of $\Delta V = 0$ implies independent variation of digit forces and correspondingly the absence of a synergy, while $\Delta V < 0$ 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). For the 0-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 for the variables such as forces, moments of force, SM, and CCI. First, to study possible effects of history on outcome, 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: SU-0, PR-0, and 0-Only). Second, to study possible changes in the mentioned variables in the process of changing the external torque, a two-way ANOVA was used with the factors *Condition-2* (two levels: SU-0 and PR-0) and *Time* (three levels: PRE, Middle, and POST; Middle refers to the mid-point of the transient state, and we used the 51st value from the 102 re-sampled data to represent it). We used the factor *Time* rather than *External Torque* because external torque values differed somewhat across subjects when measured at the mid-point of the time interval (in particular, due to different variations of the total moment of force during the PRE and POST intervals). However, effects of these two factors are expected to be the same because the load motion was at a nearly constant speed.

To study possible changes in $\sum \mathrm{Var(EV)}$, $\mathrm{Var}(\sum \mathrm{EV})$, and synergy indices, a three-way ANOVA was performed with the factor *Condition-2* (two levels: SU-0 and PR-0), *Level* (two levels: VF–TH and IF) and *Time* (three levels: PRE, Middle, and POST). One-way repeated measures ANOVA were also run to compare each variable at POST state with the factor *Condition-1*.

Before statistical analysis of the SM and synergy indices, the data were subjected to Fisher's z-transformation to mitigate the ceiling effects inherent to these variables. Pairwise comparisons were performed with Bonferroni corrections to further analyze significant effects of the studied factors. 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. The angle of the handle tilt from vertical—estimated based on the relation between the tangential forces, normal forces, and the load—was about 1.3 ± 0.28° averaged over time and across subjects and conditions. The vertical orientation of the handle was also reflected in close to zero total normal force (F^n_{TOT}) and total tangential force (F^t_{TOT}) close to the weight of the object. On average, across subjects and conditions, at the final steady-state (POST), the resultant F^n_{TOT} was 0.03 ± 0.06 N, M_{TOT} was 0.032 ± 0.012 Nm (positive values indicate pronation moment), and F^t_{TOT} was 9.83 ± 0.17 N.

The averaged across-subjects time profiles of forces produced by the thumb and virtual finger (VF) are presented in Fig. 2. The data for the 0-Only condition are shown aligned with the POST time sample with large symbols. In both SU-0 (solid traces) and PR-0 (dashed traces) conditions, F^n_{TH} and F^n_{VF} decreased smoothly with the decrease in the external torque magnitude, but the values for the SU-0 condition were consistently higher. At the final steady-state, the 0-Only condition showed the lowest force magnitudes. One-way repeated measure ANOVA confirmed that F^n_{TH} and F^n_{VF} in the SU-0 condition were significantly higher in magnitude than in the 0-Only condition ($P < 0.05$).

Changes in the total moment of force in the SU-0 and PR-0 trials were primarily produced by changes in the VF moment of force. This is illustrated in Fig. 3, which shows averaged across-subjects time profiles of the moment of force produced by the thumb, $M_{TH,}$ and moment of force

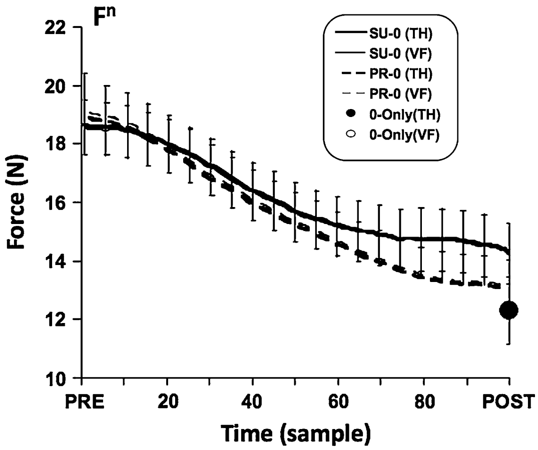

Fig. 2 Changes in the normal forces (F^n) of the thumb (TH) and virtual finger (VF). Averaged across-subjects data are shown with *standard error bars* plotted for every fifth time sample. The time scale shows the two steady-states (PRE and POST) and the 100 re-sampled points during the torque change period. The *solid lines* show the data for the SU-0 condition, and the *dashed lines* show the data for the PR-0 condition. The data for the 0-Only condition are shown with *large symbols* aligned with the POST time sample; note that the *lines* and *symbols* for the thumb and VF nearly overlap

produced by VF, M_{VF}. Note the large magnitude of changes in M_{VF} and the relatively modest changes in M_{TH}.

Another way to analyze the total moment of force is to consider the contribution of the moments produced by the normal and tangential forces (cf. Zatsiorsky et al. 2002). The time profiles of the moments of force produced by the normal and tangential forces are illustrated in Fig. 4. The normal forces, on average, produced twice as large moment magnitudes as the tangential forces.

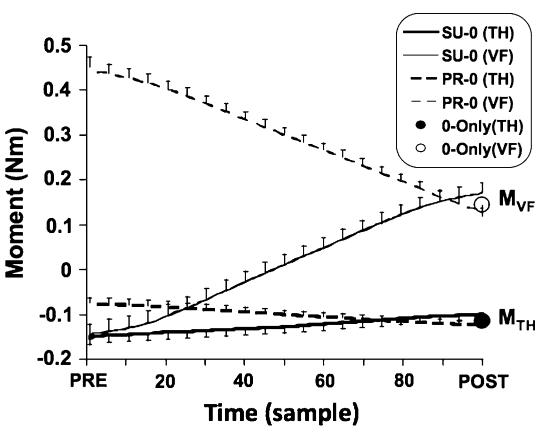

Fig. 3 Changes in the moment of forces (M) produced by the thumb (TH) and virtual finger (VF). Averaged across-subjects data are shown with *standard error bars* plotted for every fifth time sample. The time scale shows the two steady-states (PRE and POST) and each of the 100 re-sampled points during torque change. The *solid lines* show the data for the SU-0 condition, and the *dashed lines* show the data for the PR-0 condition. The data for the 0-Only condition are shown with *large symbols* aligned with the POST time sample

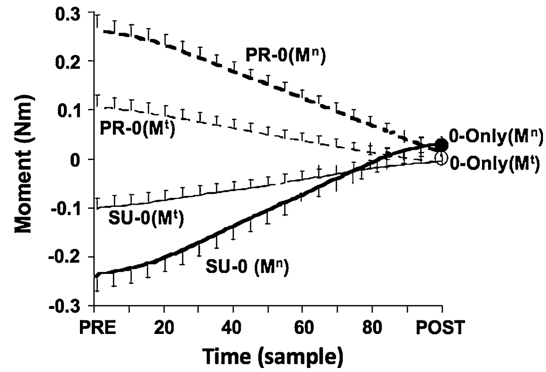

Fig. 4 Changes in the moment of normal forces (M^n) and moment of tangential force (M^t). Averaged across-subjects data are shown with *standard error bars* plotted for every fifth time sample. The time scale shows the two steady-states (PRE and POST) and each of the 100 re-sampled points during torque change. The *solid lines* show the data for the SU-0 condition, and the *dashed lines* show the data for the PR-0 condition. The data for the 0-Only condition are shown with *large symbols* aligned with the POST time sample

Two-way ANOVA *Condition-2* × *Time* on M_{VF}, M_{TH}, M^n, and M^t showed significant effects of *Condition-2* ($F_{1,14} > 14$; $P < 0.01$) and a significant *Condition-2* × *Time* interaction ($F_{1,14} > 93$; $P < 0.01$) for each of the variables. Pair-wise comparisons confirmed the differences between these two conditions at PRE, Middle, and POST for M_{VF}, M_{TH}, and M^n ($P < 0.05$) and at PRE and Middle for M^t. The effects of *Condition-2* reflected the overall higher moment of force magnitudes for the PR-0 condition, while the interaction reflected the changes in the moments of force in opposite directions under the two conditions. Compared with the 0-Only condition at the final steady-state, there were no differences among the three conditions for any of the four variables.

Figure 5 illustrates changes in the safety margin (SM) prior to (panel a) and after z-transformation (SM_z, panel b). SM decreased from a higher value in the PR-0 condition and reached a value close to those in the other two conditions by the end of the trial. In contrast, there were only minor changes in SM over the trial duration in the SU-0 condition. Two-way repeated measure ANOVA showed significant effects of *Condition-2* ($F_{1,7} = 40.71$; $P < 0.001$), *Time* ($F_{2,14} = 36.69$; $P < 0.001$), and *Condition-2* × *Time* interaction ($F_{2,14} = 111.13$; $P < 0.0001$). Pair-wise comparisons confirmed significant ($P < 0.05$) differences at each time, PRE, Middle, and POST, between the SU-0 and PR-0 conditions. They also confirmed significant differences among all three time samples for the PR-0 condition and between the POST and Middle samples for the SU-0 condition. At the final steady-state, there was no significant difference among the three conditions according to the one-way repeated measures ANOVA.

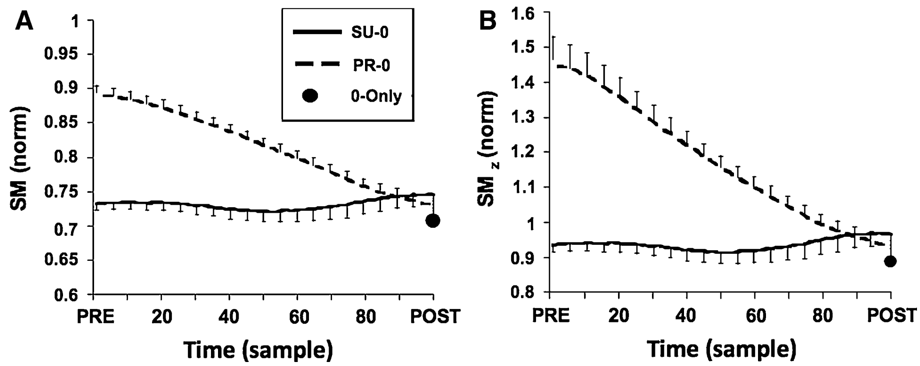

Fig. 5 Changes in the safety margin (SM) and in the z-transformed SM values (SM_z) averaged across subjects. *Standard error bars* are plotted for every fifth time sample for SM_z. The time scale shows the two steady-states (PRE and POST) and each of the 100 re-sampled points during torque change. The *solid lines* show the data for the SU-0 condition, and the *dashed lines* show the data for the PR-0 condition. The data for the 0-Only condition are shown with *large symbols* aligned with the POST time sample

The co-contraction index (CCI) was computed as the normalized difference between the moment of force produced by the fingers that acted in the direction of the VF moment of force (agonists) and those that acted against the directions on the VF moment of force (antagonists). Figure 6 illustrates the time profile of the co-contraction index (CCI) in the SU-0 and PR-0 conditions. CCI in the SU-0 condition increased during the first half of trial, reached its peak near the middle of trial, and then decreased. In contrast, CCI in the PR-0 condition increased continuously over time. These differences were supported by a two-way repeated measures ANOVA that showed significant effect of *Condition-2* ($F_{1,7} = 72.38$; $P < 0.001$) and a significant *Condition-2* × *Time* interaction ($F_{2,14} = 47.81$; $P < 0.001$). Pair-wise comparisons with Bonferroni correction confirmed that the differences between the SU-0 and PR-0 conditions were significant at PRE and in the middle of the trial, but not at POST ($P < 0.05$).

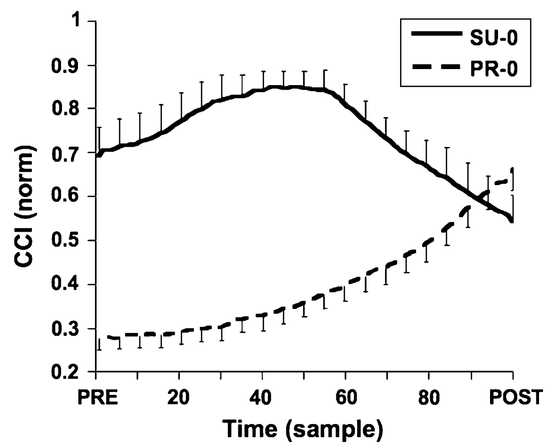

Fig. 6 Changes in the co-contraction index (CCI). Averaged across subjects values with *standard error bars* plotted for every fifth time sample. The time scale shows the two steady-states (PRE and POST) and each of the 100 re-sampled points during torque change. The *solid lines* show the data for the SU-0 condition, and the *dashed lines* show the data for the PR-0 condition. The data for the 0-Only condition are shown with *large symbols* aligned with the POST time sample

Variance analysis

The index of co-variation (ΔV) was computed as the normalized difference between the sum of the variances of elemental variables, $\sum \text{Var(EV)}$, and the variance of their summed output, $\text{Var}(\sum \text{EV})$, computed across all the trials at each time sample for each subject and each condition separately. We analyzed these three indices of variance for F^n, F^t, and M_{TOT} at both levels of the assumed control hierarchy, VF–TH and IF. The ΔV indices were subjected to the Fischer z-transformation before statistical analyses.

Figures 7 and 8 illustrate the time profile of $\sum \text{Var(EV)}$ and $\text{Var}(\sum \text{EV})$, respectively. There are both commonalities and differences across the trends. For most comparisons, the values of $\text{Var}(\sum \text{EV})$ were about an order of magnitude smaller than the values of $\sum \text{Var(EV)}$. This result suggests predominantly negative co-variation among the elemental variables for both levels of analysis, for each of the variables (F^n, F^t and M_{TOT}), and for both conditions. The notable exception is F^n at the IF level, for which $\text{Var}(\sum \text{EV})$ was consistently larger than $\sum \text{Var(EV)}$. In other words, it suggests strong synergies stabilizing each of the variables at all time samples.

Most variables show a trend to decrease over the trials for both PR-0 and SU-0 conditions at both levels. The time effect was supported by the three-way repeated measures ANOVA on $\sum \text{Var(EV)}$ for all variables, effect of *Time* (F value ranging from 7.2 to 11, $P < 0.05$). For $\text{Var}(\sum \text{EV})$, the effect of *Time* was confirmed for F^n and M_{TOT} (F value ranging from 5.08 to 5.28, $P < 0.01$). For F^n, the $\sum \text{Var(EV)}$ values were significantly higher at the VF–TH level supported by a three-way ANOVA *Condition* × *Time* × *Level*; effect of *Level* ($F_{1,7} = 71.61$;

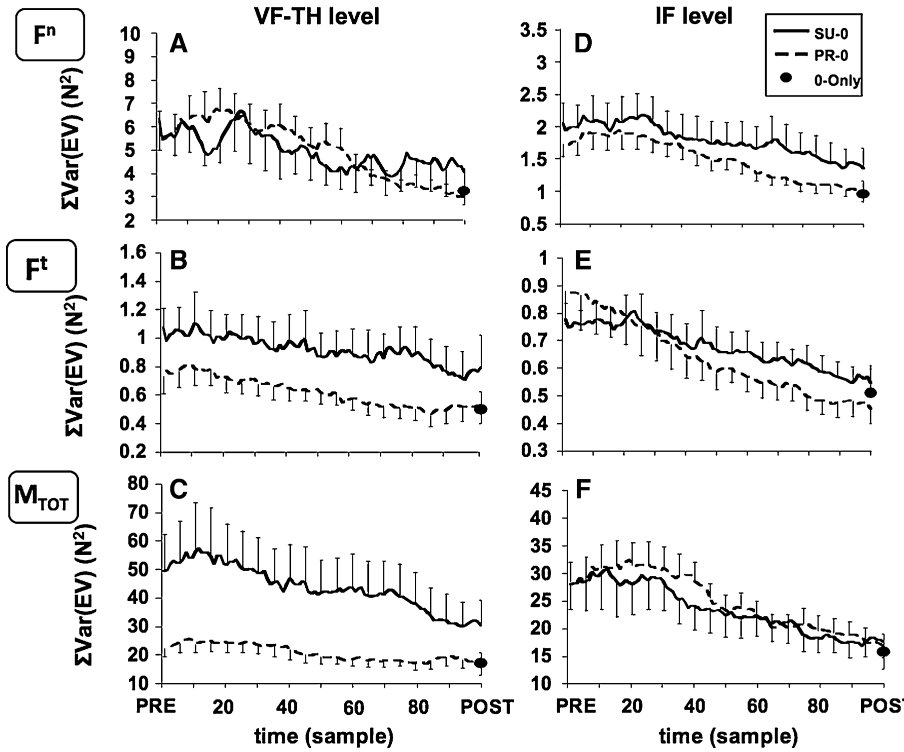

Fig. 7 Sum of the variances of the elemental variables, $\sum \mathrm{Var(EV)}$, computed at the two levels of the assumed hierarchy, the VF–TH level (*left panels*) and the IF level (*right panels*) with *standard error bars*. The *top panels* (**a**, **d**) show the indices for the normal forces, the *middle panels* (**b**, **e**) for the tangential forces, and the *bottom panels* (**c**, **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 during torque change. The *solid lines* show the data for the SU-0 condition, and the *dashed lines* show the data for the PR-0 condition. The data for the 0-Only condition are shown with *large symbols* aligned with the POST time sample. Averaged across-subjects data are presented

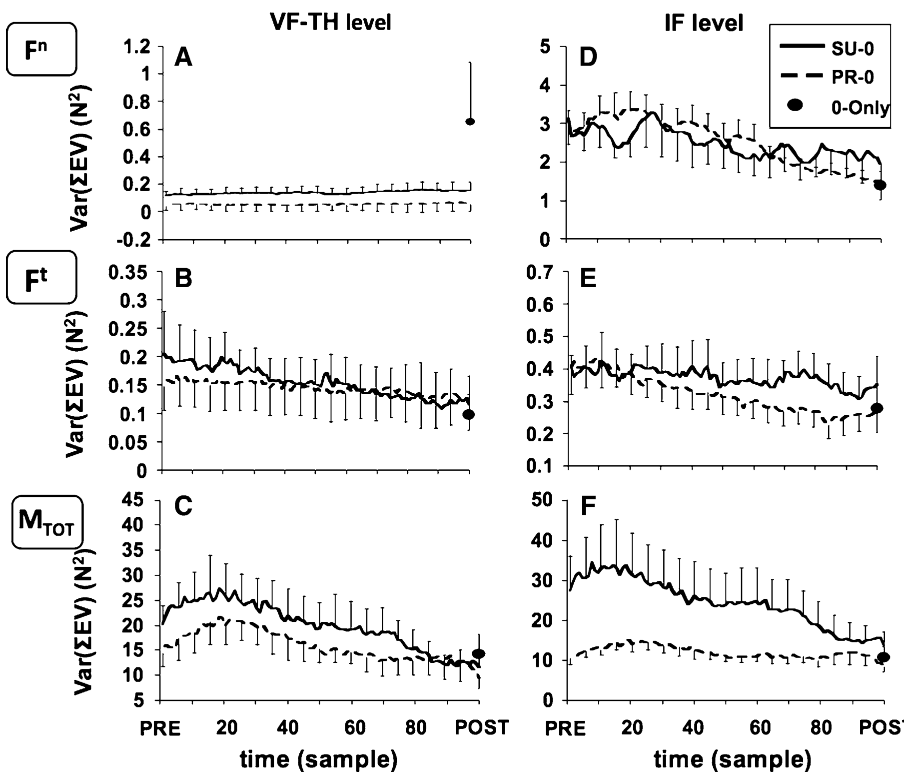

Fig. 8 Variance of the combined output of the elemental variables, $\mathrm{Var}(\sum \mathrm{EV})$, computed at the two levels of the assumed hierarchy, the VF–TH level (*left panels*) and the IF level (*right panels*) with standard error bars. The *top panels* (**a**, **d**) show the indices for the normal forces, the *middle panels* (**b**, **e**) for the tangential forces, and the *bottom panels* (**c**, **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 SU-0 condition, and the *dashed lines* show the data for the PR-0 condition. The data for the 0-Only condition are shown with *large symbols* aligned with the POST time sample. Averaged across-subjects data are presented

$P < 0.001$). Similar three-way ANOVAs showed that there were interaction effects *Condition* × *Level* for both F^t and M_{TOT} ($F_{1,7} > 8.2$; $P < 0.05$) which reflected higher $\sum \mathrm{Var(EV)}$ in the SU-0 condition at the VF–TH level, but lower at the IF level. At the final state, there were no differences among the three conditions: no effects in one-way repeated measure ANOVAs for any variables at either level.

For F^n, three-way repeated measure ANOVA, *Condition* × *Time* × *Level,* confirmed that Var($\sum$EV) was significantly higher at the IF level and that this variable dropped over time only at the IF level, supported by effects of *Level* ($F_{1,7} = 110.76$; $P < 0.001$) and a *Time* × *Level* interaction ($F_{2,14} = 5.24$; $P < 0.05$). For F^t, Var($\sum$EV) was significantly higher at the IF level, effect of *Level* ($F_{1,7} = 9.23$; $P < 0.05$) without other significant effects. At the final steady-state (POST), there were no significant differences among the three conditions according to one-way repeated measure ANOVAs.

The averaged across-subjects ΔV_z values are shown in Fig. 9. Only ΔV_z for F^n at the VF–TH level showed a significant change (drop) with time: effect of *Time* in a three-way repeated measures ANOVA ($F_{2,14} = 10.46$; $P < 0.05$). Pair-wise contrasts confirmed a significant difference between the PRE and POST values. The magnitude of ΔV_z for F^n was larger at the VF–TH level, while ΔV_z for M_{TOT} was smaller at the VF–TH level compared to the IF level. The effect of *Level* was confirmed for both F^n and M_{TOT} (F value ranges from 8.5 to 268.2; $P < 0.05$). In addition, for $M_{TOT,}$ the magnitude of ΔV_z was larger in the SU-0 condition (compared to the PR-0 condition) at the VF–TH level, but smaller at the IF level, confirmed by a significant interaction *Condition* × *Level* ($F_{2,14} = 7.91$; $P < 0.05$). At the final steady-state, there was no significant effect of *Condition-1* for any variable at either level.

Discussion

The experiments provided support for two of the four specific hypotheses formulated in the Introduction. In particular, as in an earlier study (Sun et al. 2011), we did observe non-monotonic changes in the synergy indices during the conditions with changes in the external torque (PR-0 and SU-0) in contrast to relatively monotonic changes in variance indices computed for most variables (see Figs. 7, 8, 9). We also observed signs of a trade-off between synergy indices computed at different levels of the hypothetical two-level hierarchy (Gorniak et al. 2007a, b; 2009). If one of the conditions, compared to the other condition, showed higher ΔV indices computed for a certain performance variables at the higher level (VF–TH level), at the lower level, the relationship between the synergy indices switched (Fig. 9).

The other two hypotheses were not supported by the findings. Indeed, we found a trend toward higher safety margin indices for the two conditions with external torque change as compared to the condition without a torque change (0-Only). This finding is opposite to the observations in the earlier study with changes in the weight of the hand-held object (Sun et al. 2011). Besides, we found a strikingly unequal sharing of the total moment of force between the moment produced by the normal forces and the moment produced by the tangential forces. This finding

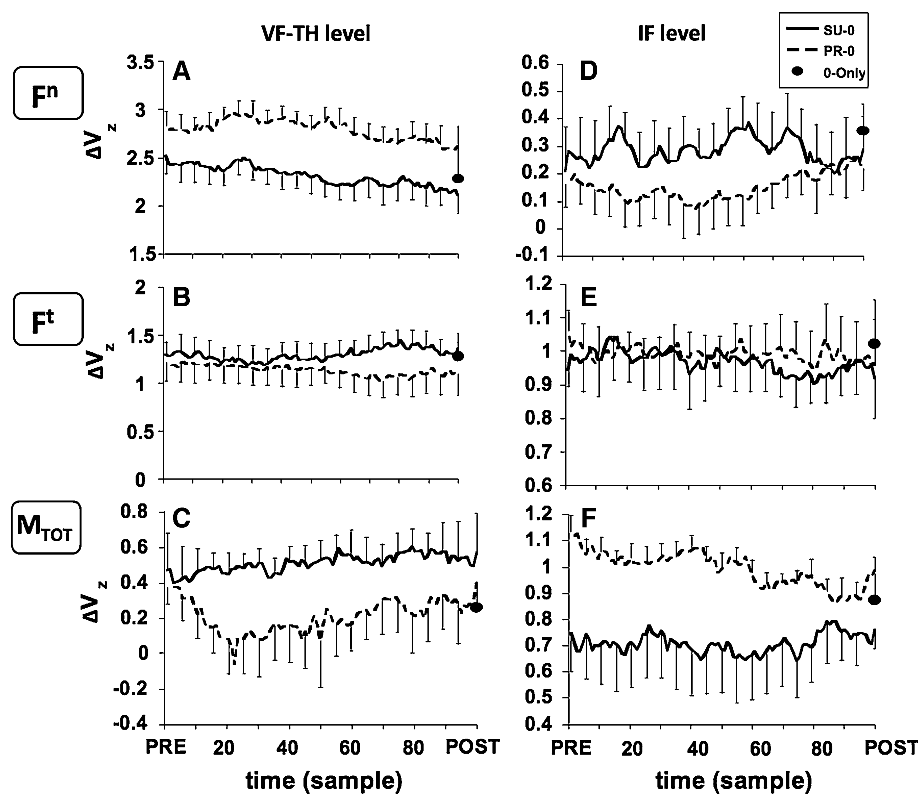

Fig. 9 Indices of *z*-transformed co-variation of elemental variables, $\Delta V_{z,}$ computed at the two levels of the assumed hierarchy, the VF–TH level (left panels) and the IF level (*right panels*) with *standard error bars*. The *top panels* (**a**, **d**) show the indices for the normal forces, the *middle panels* (**b**, **e**) for the tangential forces, and the *bottom panels* (**c**, **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 SU-0 condition, and the *dashed lines* show the data for the PR-0 condition. The data for the 0-Only condition are shown with *large symbols* aligned with the POST time sample. Averaged across-subjects data are presented

is not easily compatible with earlier reports on the nearly equal sharing of the total moment between these two components (Zatsiorsky et al. 2002, 2003).

Another unexpected finding is the differences between the PR-0 and SU-0 tasks in the patterns of several of the performance variables that suggest important differences in the control of pronation and supination efforts. Further in the Discussion, we address implications of these findings for a number of issues including the control of multi-digit tasks, synergies in hierarchically organized systems, and possible sources of the differences in the control of pronation and supination moments of force.

Mechanics of applying a rotational effort

The total moment of force applied to the handle may be represented at the sum of four components produced by the thumb and VF:

$$M_{\mathrm{TOT}} = M^n_{\mathrm{TH}} + M^t_{\mathrm{TH}} + M^n_{\mathrm{VF}} + M^t_{\mathrm{VF}} \quad (10)$$

where the subscripts refer to the thumb, and VF and the superscripts refer to the moments produced by normal (n) and tangential (t) forces. Since the lever arm for both tangential forces is constant, changes in the M^t components may only be produced by redistributing the total tangential force (which had to be equal to the weight of the object) between the thumb and VF. There is little room for changing the point of application of the normal force of the thumb (about ±0.005 m according to Zatsiorsky et al. 2002; Shim et al. 2003). On the other hand, redistributing the normal force of the VF among the four fingers allows for changing the point of application of this force over a relatively large range corresponding to the distance between the index and little finger force sensors.

We view the geometry of the prismatic grasp and the changes in the external torque as two major factors that led to the following two observations. First, we saw much larger adjustments of the moment of force produced by the VF as compared to the moment of force produced by the thumb (Fig. 3). Second, there were much larger adjustments in M^n as compared to the adjustments in M^t (Fig. 4). The more than twofold difference between M^n and M^t at all times when the external torque was significantly different from zero contrasts the earlier observations of nearly equal contributions of M^n and M^t to the total moment of force (Zatsiorsky et al. 2002, 2003). This may be due to several factors such as the geometry of the handle, the actual load/torque magnitudes, and the time-varying torque. In some of the earlier studies, the handle was wider such that the horizontal distance between the sensor surfaces was, on average, about 0.068 m (Shim et al. 2003), resulting in larger lever arms for the tangential forces. In other studies, however, the handle width was about the same as in this study (Zatsiorsky et al. 2002, 2003). In some of the mentioned earlier studies (e.g., Zatsiorsky et al. 2002), the distances between the centers of the force sensors in the vertical direction were 0.025 m, while in the present experiment they were 0.03 m. Hence, the moment arms of the finger normal forces were larger, and the normal finger forces of the same magnitude would generate larger moments. In the earlier mentioned studies, the load/torque ranges were broader than in the current study (we limited the magnitudes of the external load and torque to avoid fatigue). In particular, in the present study, the maximal external torque was 0.35 Nm, while in the study by Zatsiorsky et al. (2002), it was much larger, 1.5 Nm. It is also possible that the task of adjusting to the changing external torque made the subjects redistribute the moment of force such that its major portion was produced by M^n_{VF}, which was modified by changing the magnitude of the total normal force and its sharing among the four fingers.

When a person holds an object statically against a non-zero external load and a non-zero external torque, some digits may produce moment of force acting not against the external torque but in the same direction. Such moments of force have been addressed as antagonist moments, M_{ANT} (Zatsiorsky et al. 2002). One of the explanations for M_{ANT} has been the phenomenon of enslaving, that is unintended force production by fingers of a hand when other fingers produce force (Kilbreath and Gandevia 1994; Li et al. 1998; Zatsiorsky et al. 2000). For example, in our experiment, when a subject wanted to produce a moment of force into supination, purposeful normal force production by the little and ring fingers might be expected. Commands to these fingers, however, led to unintended normal force production by the index and middle fingers that generate moments of force into pronation, i.e., antagonist moments.

The two conditions, PR-0 and SU-0, were strongly asymmetrical with respect to the required moment of force produced by the VF. Indeed, the thumb tangential force always acted upward and, as such, produced a SU moment. Hence, the VF during SU-0 tasks could start with producing a SU moment (in the same direction as the moment produced by the thumb), but then, as the external torque decreased, it had to start producing a PR moment to counteract the moment produced by the thumb. This did not happen in the PR-0 condition, when VF had to produce moment always in PR. This asymmetry was reflected in the co-contraction index (CCI) computed across the four fingers with respect to the VF moment of force (Fig. 6). The PR-0 task was associated with overall smaller CCI values that increased with a decrease in the external torque. In contrast, in the SU-0 condition, the CCI values were much higher and showed a non-monotonic change with a peak in the middle of the trial. The time of the peak corresponded to the time when the direction of the VF moment of force changed; the former, on average, was 4.7 ± 0.75 s, while the latter was 4.8 ± 0.73 s.

In some earlier studies, the production of antagonist moments was associated with a particular neural strategy of increasing the rotational wrist apparent stiffness (see Latash and Zatsiorsky 1993); in particular, elderly persons show increased antagonist moments (Shim et al. 2004a, b) possibly related to their decreased ability to produce desired rotational hand actions (Olafsdottir et al. 2007). In our study, it was also possible that the difference between the SU-0 and PR-0 trials was associated with the SU moment direction associated with larger variability of the mechanical variables and lower mechanical stability in the PR-SU direction (Shim and Park 2007; Zhang et al. 2009; see also later in the "Discussion") and resulting in purposeful larger M_{ANT} production. On the other hand, as the previous analysis shows, the difference could be due to purely mechanical differences between the tasks due to the asymmetrical involvement of the thumb into the total moment of force production.

Adjustments of multi-digit synergies in the two-level hierarchy

Analysis of synergies at the VF–TH and IF levels of the hierarchy in earlier studies showed a trade-off between the indices of synergies at the two levels: A large synergy index at the higher level was associated with a low index at the lower level (Gorniak et al. 2007a, b, 2009). This relation between the synergy indices may be expected from the method of computation of the index. Indeed, at the higher level, large "good variability" (V_{GOOD}, variance that does not affect the important performance variable) increases the synergy index. On the other hand, large V_{GOOD} means that variance of both thumb and VF outputs is high. But this variance is "bad" (V_{BAD}) at the lower level of the hierarchy, where co-variation of finger forces is expected to reduce variance of the VF output. It is possible to have strong synergies at both levels (as shown in experiments for synergies stabilizing tangential force in Gorniak et al. 2009; Sun et al. 2011). For performance variables that represent the sums of elemental variables (such as F^n_{TOT} and F^t_{TOT}), this requires the following:

$$V^{VF-TH}_{GOOD} > V^{VF-TH}_{BAD}$$

$$V^{IF}_{GOOD} > V^{IF}_{BAD} = \frac{V^{VF-TH}_{GOOD}}{\sqrt{2}},$$

where the superscripts refer to the level of analysis. In a recent study (Latash et al. 2010), when the task required producing a certain value of the VF normal force on a fixed object, high synergy levels were observed at the lower level and lower indices—at the higher level. When the task changed into moving a hand-held object, the synergy indices at the higher level increased, while those at the lower level dropped. This result suggests that the relation between synergy indices at the two levels depends on task.

In our experiments, two variables, F^n and M_{TOT}, showed signs of a trade-off between the indices computed at the VF–TH and IF levels. For F^n, strong synergies ($\Delta V \gg 0$) were observed at the VF–TH level with higher ΔV magnitudes for the PR-0 condition. At the IF level, ΔV indices were close to zero with higher ΔV magnitudes for the SU-0 condition. For M_{TOT}, the relation between the ΔV indices at the two levels switched: Higher values were observed at the IF level, while at the VF–TH level, higher ΔV indices were seen for the SU-0 condition. We saw no signs of a trade-off for the third major variable, F^t; this observation confirms an earlier report on the lack of a trade-off between the VF–TH and IF levels for F^t during static prehensile tasks (Gorniak et al. 2009). This may be due to the importance of ensuring low variability of F^t across trials and at different times since this variable has to counterbalance the external load and also contributes to the production of total moment of force.

We did not find major changes in ΔV with time for any of the variables and at any level of analysis (except the modest drop in ΔV for F^n at the VF–TH level). This is in contrast to the significant effects of time on the two variance indices that were used to compute ΔV, the sum of variances of the elemental variables and the variance of their summed action ($\sum$Var(EV) and Var($\sum$EV); Figs. 7, 8). So, unlike the earlier study (Sun et al. 2011), we did not find significant time and history effects on the index of co-variation of the elemental variables, while such effects were present for the mentioned variance indices. In contrast, there were significant differences in the synergy indices between the PR-0 and SU-0 conditions showing that patterns of digit force co-variation may depend on the magnitudes of the total force and moment of force that the digits produce. This finding suggests that results of studies of multi-digit synergies (and, potentially, of other multi-element synergies) should not be generalized beyond the range of performance variables actually used in those studies.

Pronation versus supination tasks

One major difference between the PR-0 and SU-0 tasks has been mentioned earlier: The thumb contributed to SU efforts and acted against PR efforts. There have also been reports on possible differences in the neural control of tasks that require PR and SU efforts. In particular, higher peak moment magnitudes and higher synergy indices for the total moment of force have been reported for PR efforts, although in a different set of tasks that required moment of force production on a circular object (Shim et al. 2007;

Shim and Park 2007). During quick rotational actions at comparable speeds, higher normal forces were observed for actions into SU as compared to actions into PR (Zhang et al. 2009). The asymmetry between the PR and SU moments was also observed in a study of static moment of force production on a fixed object (Shim et al. 2004a, b), in studies of comfort associated with different PR–SU postures (Khan et al. 2009a, b) and in a study of the control of grasp stability during PR and SU movements (Johansson et al. 1999).

In our study, most indices showed a difference between the PR-0 and SU-0 conditions that corroborate the general idea that the SU actions are less stable (in terms of both mechanical stability and variability of mechanical variables) and performed in a less economical way. In particular, under the SU-0 condition, higher variance indices were observed for most variables, and lower synergy index values were observed at the VF–TH for F^n (Fig. 9). This condition was also characterized by higher co-contraction indices (CCI, Fig. 6) and slightly higher normal force magnitudes (Fig. 2). On the other hand, synergy indices for the SU-0 condition were higher at the VF–TH level for M_{TOT}. When safety margin values were computed (Fig. 5), it turned out that the higher normal forces in the SU-0 conditions were associated with smaller safety margins because of the higher tangential forces.

To summarize, the two studies with slow changes in the external load (Sun et al. 2011) and torque (the current study) document several previously unknown features of prehensile tasks. The commonly used characteristic of prehensile tasks, the safety margin, has been shown to depend on the task history, even when the measurements were taken at the same sets of the external load and torque. Sharing of the total moment of force between the thumb and VF (and between the moments produced by normal and tangential forces) has been shown to depend on the magnitude and direction of the external torque. The patterns of co-variation of digit forces and moments of force (prehension synergies) have been shown to depend on the history of external load changes and on the direction of external torque. These results show that characteristics of digit action and interaction in such tasks depend not only on the magnitudes of external constraints but on a variety of other factors. Prehension studies should consider all those factors.

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