

## EFFECT OF RESISTANCE TRAINING OF THE WRIST JOINT MUSCLES ON MULTI-DIGIT COORDINATION<sup>1,2</sup>

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*Summary.*—This study investigated the effects of a specific regimen of resistance training on coordinated actions of human hand digits during grasping. Participants were instructed to hold a rectangular object with all five digits and to maintain the orientation of the object against transient perturbation. Indices of co-varied actions (i.e., synergies) among multi-digit grasping and rotational actions were quantified. The index of anticipatory changes of co-varied actions among digit forces (i.e., anticipatory synergy adjustment) was also quantified, which represents the controller's ability to predict an upcoming perturbation. The synergies of both grasping force and moment stabilization increased with the training. No change in the index of anticipatory synergy adjustment with training was observed. The current results suggest that the resistance training on the wrist could be an effective way to enhance both voluntary muscle force/torque production capability and ability to stabilize task performances during multi-digit prehensile tasks.

Sport performances, as well as many everyday activities requiring the use of the hand and wrist, are affected by the strength and the dexterity of wrist-finger actions (Hazelton, Smidt, Flatt, & Stephens, 1975; Imrhan & Loo, 1988; Brylinsky, Moore, & Frosch, 1992; O'Driscoll, Horii, Ness, Cahalan, Richards, & An, 1992). In particular, the unique design of the human hand enables us to perform a variety of grasping actions applying functionally effective forces by the hands and digits, which is termed prehension (Zatsiorsky, Gao, & Latash, 2003a). It has been also suggested that strength training of fingers improved the stabilization of perfor-

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<sup>2</sup>This study was supported in part by research funds of the National Research Foundation (NRF-2013004812) of Korea (to Shim), Chonbuk National University in 2013 (to Han), and a Montana NASA EPSCoR Research Infrastructure Development (RID) grant (Research Initiation Grant to Park).

mance of hand/finger actions along with higher force-production capability (Bilodeau, Keen, Sweeney, Shields, & Enoka, 2000; Keogh, Morrison, & Barrett, 2007), while fingers acted less independently following finger strength training (Olafsdottir, Zatsiorsky, & Latash, 2008; Shim, Hsu, Karol, & Hurley, 2008). Present evidence has suggested that the neuromuscular effects of strength training on fingers include neural adaptations to coordination of finger actions (i.e., motor synergy) in a redundant motor system. In a redundant motor system, the number of elemental variables such as individual finger forces is greater than the number of task-related constraints. For this reason, the controller may facilitate solution families rather than single unique solutions according to the principle of motor abundance (Gelfand & Latash, 1998; Latash, 2012). Motor synergy has been characterized and quantified by the shape of across-trial or single-trial variance (Latash, Scholz, & Schoner, 2002; Scholz, Kang, Patterson, & Latash, 2003; Friedman, Skm, Zatsiorsky, & Latash, 2009; Delis, Berret, Pozzo, & Panzeri, 2013). When synergistic actions are present in motor outputs, then the shape of variances in the space of elemental variables would be an ellipse, which shows larger "good" variance (i.e., variance of elements which does not affect a performance variable) as compared to "bad" variance (i.e., variance which does affect a performance variable). The framework of the uncontrolled manifold analysis has been used to quantify these two components of variance present in the motor outputs (Scholz & Schoner, 1999). The presence of synergy and its strength are quantified by the relative amounts of "good" and "bad" variance with respect to the total variance (i.e., a higher index number signals better synergic action of elemental variables).

Furthermore, the uncontrolled manifold analysis allows quantifying feed-forward adjustment of the indices of synergy in anticipation of a quick action (Olafsdottir, Yoshida, Zatsiorsky, & Latash, 2005) or an externally generated perturbation (Shim, Park, Zatsiorsky, & Latash, 2006). The functional purpose of synergy adjustment prior to perturbation (i.e., anticipatory synergy adjustment) is to weaken stabilization in preparation for externally imposed perturbation (Shim, *et al.*, 2006) or self-paced changes of performance variables (Ledebt, Brill, & Breniere, 1998; Olafsdottir, *et al.*, 2005; Goodman & Latash, 2006). When the timing information about an upcoming perturbation was blocked, then the anticipatory synergy adjustment was not observed (Shim, *et al.*, 2006), while the anticipatory synergy adjustment was still observed when directional information about the upcoming action alone was blocked (Zhou, Wu, Bartsch, Cuadra, Zatsiorsky, & Latash, 2013). This implies that the anticipatory synergy adjustment does not provide a positive mechanical effect (i.e., no apparent changes in important performance variables during the antici-

patory synergy adjustment, therefore zero mechanical effect) but is sensitive to timing information, inducing changes in stability in a feed-forward fashion. A series of recent studies have reported that weakened anticipatory synergy adjustments were observed in elderly people (Olafsdottir, Yoshida, Zatsiorsky, & Latash, 2007) and in patients with subcortical disorder (Park, Wu, Lewis, Huang, & Latash, 2012; Park, Lewis, Huang, & Latash, 2013), whose maximal force production capability was weaker as compared to corresponding control groups. However, it is questionable whether the index of anticipatory synergy adjustment is a strength-dependent quantity. Since there is no known evidence for the effect of hand/finger strength on the index of anticipatory synergy (Park, *et al.*, 2012, 2013; Olafsdottir, *et al.*, 2008; Zhang, Sainburg, Zatsiorsky, & Latash, 2006), the slow anticipatory synergy adjustments found in the previous studies in the elderly and in patients with neurological disorders may not be due to their weakened force-production capability. The neural process regarding feed-forward adjustment is thought to be independent of changes in physical strength, and the ability for anticipatory synergy adjustment in multi-finger actions may not be mediated by the changes in hand and finger strength after training.

Previous studies have employed a multi-finger pressing task to examine changes in strength and the coordinated actions of elemental variables following strength training (Olafsdottir, *et al.*, 2008; Shim, *et al.*, 2008). These two positive changes of the digit actions (strength and synergy) are expected to be observed in grasping actions with all five digits (i.e., multi-digit prehension) with wrist-strength training, since the motions of the wrist joint are closely related to the motions of the finger joints; also, the group of muscles used in wrist actions intersect substantially with the muscle group for finger actions (Horii, Lin, Cooney, Linscheid, & An, 1992; Su, Chou, Yang, Lin, & An, 2005; Thorsen, Occhi, Boccardi, & Ferrarin, 2006), and prehension with five-digits would be a more ecologically valid task as compared to pressing tasks.

Previous studies have suggested that there are two distinct coordinated actions (i.e., synergies) during static multi-digit prehension of both rectangular objects (Zatsiorsky, Latash, Gao, & Shim, 2004; Shim, Latash, & Zatsiorsky, 2005b) and circular objects (Shim & Park, 2007), which were presumably affected by the neuromuscular strength of hand and finger actions. One was a synergy that stabilized the grasping force, and the other was a synergy that stabilized the rotational action of the hand-held object.

Two separate sets of devices were used to examine the changes in the multi-digit coordination and torque production capability of the wrist joint following 6 wk. of wrist training. Maximal voluntary torque-production tasks were employed to quantify the wrist strength, and changes in

multi-digit coordination following the strength training were examined using static multi-digit prehension tasks against external torque-load perturbations (Shim, *et al.*, 2006). Based on the described effects of strength training, the following hypotheses were formulated.

*Hypothesis 1.* (a) Synergy indices of important performance variables (e.g., grasping force & moment of force) during static multi-digit prehension and (b) wrist strength in torque-production tasks would both increase with 6 wk. of the wrist strength training.

*Hypothesis 2.* Ability for feed-forward synergy adjustment in multi-digit synergistic anticipation of an upcoming external perturbation would not be changed after wrist strength training.

## METHOD

### *Participants*

Sixteen young men ( $M$  age=24.2 yr.,  $SD$ =6.8) with no history of upper extremity musculoskeletal injuries or neurological disorders participated in the study as research participants. Eight participants were randomly assigned into each of two groups, wrist training ( $n=8$ ) and control groups ( $n=8$ ). All individuals were right-handed, according to the definitions in the Edinburgh Handedness Inventory (Oldfield, 1971). None of the subjects had a previous history of neuropathies or traumas to the upper extremities. Prior to the experiment, testing procedures of the study were explained and all participants signed a consent form approved by the university's internal review board (IRB).

### *Equipment*

A hammer type device with a vertical shaft (Fig. 1A) was used to perform resistance training for the wrist. The length of the shaft was 28 cm, and the weight of the hammer varied depending on the maximal voluntary torque values of individual subjects.

For individual finger forces and moments acquisition, five 6-component (three force and three moment components) transducers (Nano-17s, ATI Industrial Automation, Garner, NC, USA) were attached to an aluminum handle (Fig. 2A). The validity of a measurement tool was estimated from the data provided by the vendor of force/torque sensors. The uncertainty (i.e., measurement error or accuracy) estimates of each sensor ranged between 0.03 N and 0.05 N for force and between 0.02 N cm and 0.06 N cm for torque. The uncertainty values of the current estimation were similar to the values reported in the previous studies (Shim, Latash, & Zatsiorsky, 2003; Zatsiorsky, *et al.*, 2004). One six-component (three po-

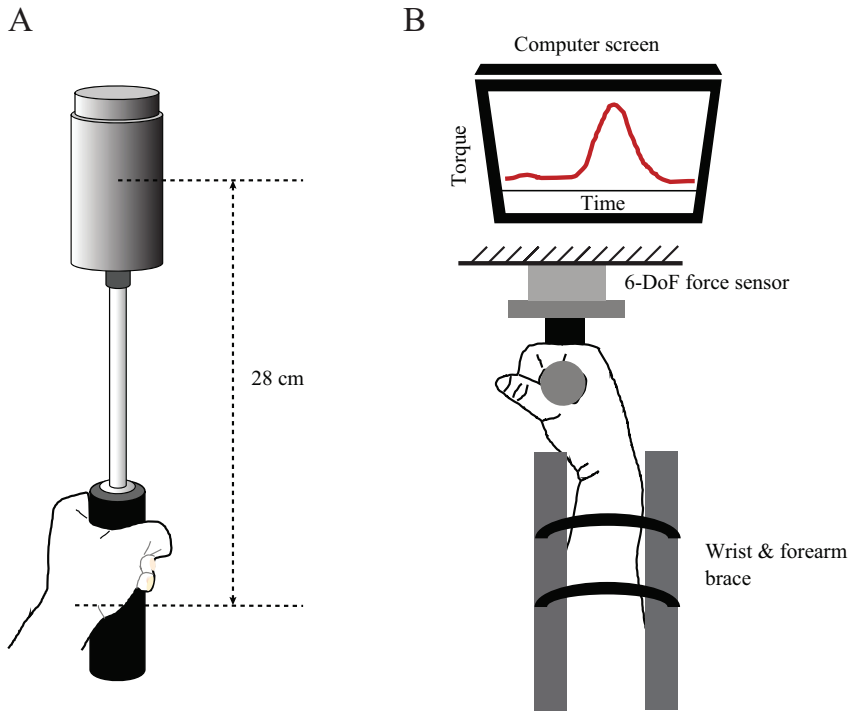


FIG. 1. A. Wrist training device. The length of the shaft was 28 cm. B. Experimental setting for wrist joint torque measurement.

sition and three angle components) magnetic tracking sensor (Polhemus Liberty, Rockwell Collins Co., Colchester, VT, USA) was mounted to the top of the aluminum handle to measure the linear and angular positions of the handle and to provide feedback concerning the linear or angular positions of the handle during the tasks. Three loads (0.30 kg each) were attached at three different positions (i.e., left, center, and right) of the beam. The load at the left location was attached with a cotton thread so that this load was used to provide transient and concomitant load/torque perturbation. The other two loads were attached with bolt-nut structures. A single-component force sensor (Model 208A03, Piezotronics, Inc.) was attached to the bottom of the left load connected by a thread to the handle to detect the time of the perturbation initiation. The sensors were aligned in the  $y$ - $z$  plane (Fig. 2A). The sampling frequency was set at 400 Hz. The data were acquired by customized LabVIEW programs and MatLAB programs were written for data processing.

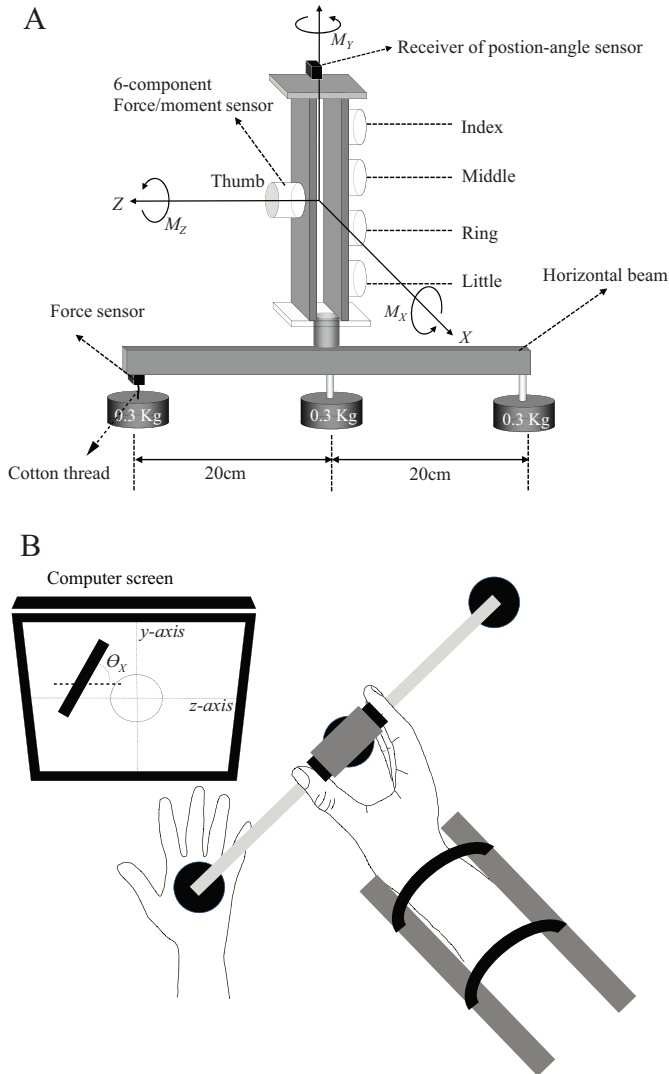


FIG. 2. A. The customized handle. The force-moment sensors shown as white cylinders were attached to two vertical aluminum bars. The receiver of a magnetic position-angle sensor, marked as a small black cube, was attached to the plastic base affixed to the top of the handle.  $M_X$ ,  $M_Y$ , and  $M_Z$  are moments produced by the digits about X-, Y-, and Z-axes, respectively. B. Participants were instructed to place each digit on the designated sensor (i.e., for thumb, index, middle, ring, and little fingers) and keep all digits on the sensors during trials. The right wrist and forearm were secured with Velcro straps. Participants monitored the angular position of the handle during trials. The load at left, which was connected by a thread to the handle, was lifted either by an experimenter's hand (experimenter-triggered condition) or by the participant's left hand (self-triggered condition).

### Procedure

*Wrist strength training.*—The resistance training protocol was applied to the training group only. During the training, the training group participants were instructed to perform six different wrist movements (e.g., flexion-extension, pronation-supination, ulnar-radial deviation) at the controlled slow speed (Table 1) using the hammer type training device (Fig. 1A). The weight of the hammer was adjusted according to the maximal voluntary torques of the individual subjects by matching 70% of the maximal voluntary torque for each wrist movement. All participants performed training five days per week for 6 wk. except on the days of laboratory tests (e.g., the wrist strength test and the multi-digit prehension test). The strength training was performed in the laboratory; the experimenter managed the training schedule and ensured correct training. The repetition workloads in a single set were gradually increased every 2 wk. (Table 1). In addition, the participants were instructed to maintain their usual dietary habits throughout the 6 wk. of training.

*Wrist strength test.*—The wrist strength test was conducted every 2 wk. during the 6 wk. training period (Table 1) for both groups. Isometric maximum wrist torque about the wrist joint was assessed before and during the 6 wk. training. The participants sat on a chair, and placed their right upper arm into a wrist-forearm brace fixed to a table (Fig. 1B). The participants were instructed to produce maximal voluntary torque for flexion, extension, pronation, supination, radial deviation, and ulnar deviation efforts. The participants were instructed to produce maximal voluntary torque within 8 sec. while monitoring online torque feedback. The participants relaxed immediately after reaching a maximal torque (Fig. 1B). Two trials were given to the participants for each of six directions. The sampling frequency was set at 100 Hz.

*Perturbation test during multi-digit prehension.*—The perturbation test during multi-digit prehension was conducted twice for each participant, at 0 wk. (preliminary testing) and 6 wk. (post-training test). There were four experimental conditions: before and after training, and two types of perturbation (self- and experimenter-triggered). The participants sat on a chair and placed their right upper arm into a wrist-forearm brace fixed to a table (Fig. 2B). The forearm was secured with Velcro straps. Visual feedback was given to the participants during each trial, which showed the angular position of the handle about the  $x$ -axis. Under the self-triggered perturbation condition, the participants were supposed to quickly lift with the left hand the load that was hanging by a cotton thread. During trials with experimenter-triggered unloading, a similar action was performed by the experimenter at an unpredictable time. Thus, the participants were not able to see the hand lifting the load in the experimenter-triggered condition. The task

TABLE 1  
TRAINING AND TEST TIME-LINE

Task	5 day/wk. Strength Training (sets × reps)						
	3 × 3-5		3 × 6-8		3 × 8-10		
	0 wk.	1 wk.	2 wk.	3 wk.	4 wk.	5 wk.	6 wk.
Wrist strength test	○		○		○		○
Multi-digit prehension test	○						○

*Note.*—Wrist strength training lasted for 6 wk. The wrist strength test was conducted every 2 wk. during the 6 wk. training period. The multi-digit prehension test was performed twice: at 0 wk. (preliminary test) and at 6 wk. (post-training test).

was to minimize the angular deviation of the handle from its original orientation prior to the perturbation and to restore that orientation as quickly as possible watching the computer screen. Each participant performed 15 consecutive trials with 1 min. intervals between trials. Intervals of 10 min. were given between the self- and experimenter-triggered conditions.

#### Data Analysis

A customized Matlab program (Matlab 7.4.0; MathWorks) was used to process the data. The force and torque data were digitally low-pass filtered (zero-lag, fourth-order Butterworth filter at 10 Hz cut-off). Note that the analysis of the multi-digit prehension task was limited to the frontal grasping two-dimensional plane (the  $y$ - $z$  plane in Fig. 2A).

Each participant performed maximal voluntary torque production tasks in six directions. For each directional torque production task the maximal torque was detected, and the higher maximal voluntary torque level between two consecutive attempts was selected. Furthermore, the maximal voluntary torque in each direction was normalized by the average maximal voluntary torque values of the corresponding direction at 0-wk across participants for each group (Eqn. 1). This normalization process was done separately in wrist training and control groups.

$$MVT_{NORMj}^i = (MVT_j^i / \text{average} MVT_j^{0-\text{week}}) \times 100 \quad (1)$$

where  $i = \{0 \text{ wk.}, 2 \text{ wk.}, 4 \text{ wk.}, 6 \text{ wk.}\}$  and  $j = \{\text{flexion, extension, supination, pronation, ulnar-deviation, and radial-deviation}\}$ .

*Analysis of digit force/moment co-variation (the uncontrolled manifold method; Appendix).*—The analysis was limited to static grasping in a two-dimensional plane (i.e., planar static tasks, see Zatsiorsky, *et al.*, 2004). Task-constraints were subjected to two hierarchical levels of analysis (individual finger and virtual finger). The virtual finger acted as a functional unit to



produce the same mechanical effects as combined forces and moment by all four fingers. There were three task constraints (e.g., resultant normal force, tangential force, and moment of force about the  $x$ -axis) at the virtual finger and individual finger levels for static equilibrium during multi-digit prehension tasks. The following equations describe the task constraint at the two levels of analyses.

At the virtual finger level:

$$F_N^{TOT} = F_N^{TH} + F_N^{VF} \quad (2)$$

$$F_T^{TOT} = F_T^{TH} + F_T^{VF} \quad (3)$$

$$M^{TOT} = M^{TH} + M^{VF} \quad (4)$$

At the individual finger level:

$$F_N^{VF} = F_N^I + F_N^M + F_N^R + F_N^L \quad (5)$$

$$F_T^{VF} = F_T^I + F_T^M + F_T^R + F_T^L \quad (6)$$

$$M^{VF} = M^I + M^M + M^R + M^L \quad (7)$$

where  $F$  and  $M$  stand for digit force and moment, respectively. The subscripts  $N$  and  $T$  indicate the normal tangential force components, and the superscripts  $TH$ ,  $VF$ ,  $I$ ,  $M$ ,  $R$ , and  $L$  denote the thumb, virtual finger, index, middle, ring, and little finger, respectively. Further quantitative analyses of multi-digit force- and moment-stabilization synergy were done within the framework of the uncontrolled manifold hypothesis (Scholz & Schoner, 1999). The uncontrolled manifold analysis was performed separately for each performance variable ( $F_N$ ,  $F_T$ , and  $M$ ) at each level. All the repetitive trials were aligned with respect to the time of initiation of the perturbation ( $t_0$ ), which was detected in the force change data from the single-component force sensor at the bottom of the load. The previous uncontrolled manifold analysis on multi-digit pressing employed the mode data (Danion, Schoner, Latash, Li, Scholz, & Zatsiorsky, 2003) as elemental variables by removing inter-digit dependency, called finger-force enslaving (a phenomenon of unintended force production by non-task fingers during a task finger-force production; see Reilly & Hammond, 2000; Zatsiorsky, Li, & Latash, 2000). In the current uncontrolled manifold analysis, digit forces and moments as elemental variables were used rather than mode data because of the technical difficulties inherent in computing the index of inter-digit dependency

due to translation and rotation of the hand-held object during multi-digit prehension tasks. Two variance components were quantified across the aligned repetitive trials at every moment in time: (1) variance which does not change the average value of the selected performance variables ( $V_{UCM}$  or  $V_{GOOD}$ ), and (2) variance that changed the selected performance variables resulting in the performance error ( $V_{ORT}$  or  $V_{BAD}$ ). An index of synergy, which reflects the relative magnitude of  $V_{GOOD}$  and  $V_{BAD}$  per degree of freedom with respect to the total variance ( $V_{TOT}$ ) is shown in Equation 8:

$$\Delta V(t) = \frac{\left( V_{UCM}(t) / DoF \text{ of } UCM \right) - \left( V_{ORT}(t) / DoF \text{ of } ORT \right)}{\left( V_{TOT}(t) / DoF \text{ of } TOT \right)}, \quad (8)$$

where  $DoF$  and  $V_{TOT}$  stand for the degrees of freedom and the total variance, respectively, and  $V_{TOT} = V_{UCM} + V_{ORT}$ . Note that the uncontrolled manifold analysis assumes that various combinations of elemental variables across repetitive trials (i.e., variability of elemental variables) are equally able to ensure a successful performance. Because  $\Delta V$  had computational boundaries depending on the number of elemental variables involved in the computation,  $\Delta V$  was log-transformed with Fischer transformation ( $\Delta V_z$ ). The steady-state value of  $\Delta V_z$  was computed for "before" and "after" the perturbation separately. The time periods of before and after perturbation were set at  $-1000$  msec. to  $-800$  msec. and  $+2000$  msec. to  $+2200$  msec. with respect to  $t_0$ . For the quantification of the time of anticipatory synergy adjustment ( $t_{ASA}$ ), the average and  $SD$  values of  $\Delta V_z$  at the steady state before perturbation ( $-1000$  msec. to  $-800$  msec. before  $t_0$ ) were computed. Then,  $t_{ASA}$  was defined as the time when  $\Delta V_z$  dropped below its average steady-state value by more than two standard deviations ( $SDs$ ).

### Statistical Analyses

The power analysis was performed based on  $\Delta V$  values reported in previous studies. Typical changes of  $\Delta V$  reported with practice or training in adults were about  $0.4$ – $0.6$  with  $SDs$  of about  $0.1$ – $0.3$  (Kang, Shinohara, Zatsiorsky & Latash, 2004; Shim, *et al.*, 2008). The effect size in those studies was larger than  $0.7$ . Assuming a similar effect size for the current study, 16 participants were trained and tested, 8 in each group. *Post hoc* calculation of the effect size for all comparisons was performed, and the effect size of all significant comparisons for the training effect was  $>0.60$ . The standard descriptive statistics are presented as means and standard errors. For the repetitive measures of the three important performance

variables,  $F_{N'} F_{T'}$  and  $M_{TOT'}$  the intra-class correlation coefficients (ICC) as an index of test-retest reliability were estimated (ICC = .79 for  $F_{N'}$   $p < .001$ ; ICC = .72 for  $F_{T'}$   $p < .001$ ; ICC = .66 for  $M_{TOT'}$   $p < .001$ ). ANOVAs with repeated-measures were used to explore how the main outcome variables ( $MVF_{NORM}$ ,  $\Delta V_Z$  of  $F_{N'}$ ,  $F_{T'}$  and  $M_{TOT'}$ ) at the virtual finger and individual finger levels are affected by Group (wrist training and control), Time (0 and 6 wk.; or 0, 2, 4, and 6 wk.), Trigger (self- and experimenter-triggered), Perturbation (before and after perturbation), and Direction (flexion, extension, pronation, supination, ulnar-, and radial-deviation). ANOVAs were run separately for each of the variables mentioned above, and a set of factors was selected for particular comparisons. A Greenhouse-Geisser adjustment was used to reduce the degrees of freedom in case of violation of the sphericity test (Mauchly's sphericity test). Significant effects were further explored with Mann-Whitney tests with Bonferroni adjustments to  $p$  for multiple comparisons. Since the  $\Delta V$  variables had computational boundaries depending on the number of elemental variables in the computations, these values were transformed using Fisher's  $z$ -transformation for statistical comparisons. Statistical significance was set at  $p \leq .05$ . All statistical tests were performed using SPSS 19.0 (SPSS Inc., Chicago, IL).

## RESULTS

### *Maximal Voluntary Torque (MVT) Production*

In general, the wrist training group showed a significant increase in the normalized isometric maximal voluntary torque ( $MVT_{NORM}$ ) in all six directions after 6 wk. of the training, whereas  $MVT_{NORM}$  remained unchanged in the control group (Fig. 3). In particular, the significant  $MVT_{NORM}$  increase in the wrist training group was observed after 2 wk. in all six directional  $MVT_{NORM}$  ( $p < .05$ ) except supination and pronation. The significant training effects on the supination and pronation  $MVT_{NORM}$  were observed at 4 wk. (Fig. 3C & D). The strongest training effects on  $MVT_{NORM}$  were observed in flexion, radial deviation, ulnar deviation, and extension in which the maximal voluntary torques increased by about 68.37%, 56.56%, 44.7%, and 37.63%, respectively. The supination and pronation maximal voluntary torques showed relatively weaker training effect (increased by about 27.65% for pronation; 22.82% for supination) as compared to the training effect of other directional  $MVT$ s.

A three-way repeated-measures ANOVA performed on  $MVT_{NORM}$  with factors Direction (six levels), Group (wrist training and control), and Time (0, 2, 4, 6 wk.) showed significant main effects of Group ( $F_{1,14} = 12.03$ ,  $p < .001$ ) and Time ( $F_{1.84,25.72} = 19.61$ ,  $p < .001$ ) with significant interactions of Time  $\times$  Group ( $F_{1.84,25.72} = 34.18$ ,  $p < .0001$ ), Time  $\times$  Direction ( $F_{4.80,67.22} = 1.91$ ,  $p < .05$ ), and Time  $\times$  Group  $\times$  Direction ( $F_{4.80,67.22} = 2.28$ ,  $p < .01$ ). The signifi-

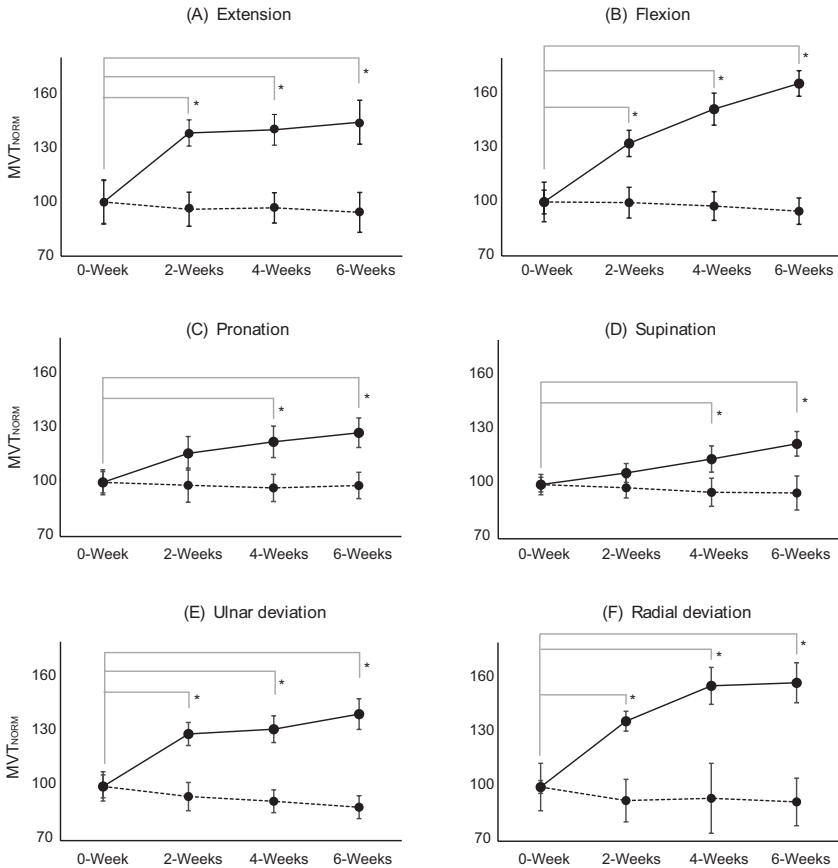


FIG. 3. Normalized maximal voluntary torque ( $MVT_{NORM}$ ) of extension (A), flexion (B), pronation (C), supination (D), ulnar deviation (E), and radial deviation (F) for 6 wk. of wrist training in the wrist training (solid line) and control (dotted line) groups. The wrist strength test was conducted every 2 wk. during the 6 wk. training period. \* $p < .05$ .

cant two-way and three-way interactions reflected the fact that (a) the significant effects of Time were observed in the wrist training group only, (b) the significant difference between two groups was observed at 2, 4, and 6 wk., and (c) the training effect in the wrist training group varied with the maximal voluntary torque directions. *Post hoc* comparisons in the wrist training group confirmed that  $MVF_{NORM}$  at 6 wk. was always larger than that at 0 wk. for all six torque directions ( $p < .05$ ), and the training effect of  $MVF_{NORM}$  in flexion, radial deviation, ulnar deviation > extension > supination, pronation ( $p < .05$ ).

### Synergy Analysis of Multi-digit Prehension Tasks

The uncontrolled manifold analyses were performed at two levels: the virtual finger level and the individual finger level. In addition, the uncontrolled manifold analyses were applied to normal forces ( $F_N$ ), tangential forces ( $F_T$ ), and moment of forces ( $M_{TOT}$ ) at each level of analysis.

*Virtual finger level.*—The indices of the steady-state synergies at the virtual finger level for the moment of force ( $\Delta V_M$ ) and normal force ( $\Delta V_{Fn}$ ) showed significant changes following training in the wrist training group, which was not observed in the control group (Fig. 4A & C). Both  $\Delta V_{Fn}$  and  $\Delta V_M$  increased with strength training. Steady-state  $\Delta V_M$  remained constant after the perturbation, while the steady-state value of  $\Delta V_{Fn}$  after the perturbation was smaller than the value before the perturbation. These findings were supported by four-way repeated ANOVAs separately on  $\Delta V_{Fn}$ ,  $\Delta V_{Fn'}$  and  $\Delta V_M$  at steady-state with factors Group (wrist training and control), Time (0 and 6 wk.), Perturbation (before and after), and Trigger (self- and experimenter-triggered), which showed the significant effect of Time on  $\Delta V_{Fn}$  and  $\Delta V_M$  ( $F_{1,14} = 12.13$ ,  $p < .01$  for  $\Delta V_{Fn}$ ;  $F_{1,14} = 7.12$ ,  $p < .05$  for  $\Delta V_M$ ) with significant Time  $\times$  Group interactions ( $F_{1,14} = 6.83$ ,  $p < .05$  for  $\Delta V_{Fn}$ ;  $F_{1,14} = 5.14$ ,  $p < .05$  for  $\Delta V_M$ ). The significant Time  $\times$  Group interactions on  $\Delta V_{Fn}$  and  $\Delta V_M$  reflected the fact that decreased  $\Delta V_M$  and increased  $\Delta V_{Fn}$  after 6 wk. were significant in the wrist training group only, which was confirmed by *post hoc* comparisons ( $p < .05$ ). The main effect of Perturbation was significant only on  $\Delta V_{Fn}$  without an interaction ( $F_{1,14} = 12.85$ ,  $p < .01$ ).

*Individual finger level.*—In the wrist training group,  $\Delta V_{Fn}$  decreased while  $\Delta V_M$  increased with 6 wk. of training (Fig. 4B & D). In contrast,  $\Delta V_{Fn}$  and  $\Delta V_M$  in the control group remained unchanged after 6 wk. There was no significant change in  $\Delta V_{Fn}$  after 6 wk. for either the wrist training or control groups. After quick changes in  $\Delta V$  followed by the perturbation (given at  $t_0$ ), the steady-state value of  $\Delta V$  was restored within 1.5 sec. to 2.5 sec. The steady-state value of  $\Delta V_M$  after the perturbation was larger than the value before the perturbation, whereas there was no significant change in the steady-state values of  $\Delta V_{Fn}$  before and after the perturbation.

Four-way repeated ANOVAs were run separately on  $\Delta V_{Fn}$ ,  $\Delta V_{Fn'}$  and  $\Delta V_M$  at steady-state with factors Group (wrist training and control) and Time (0 and 6 wk.), Perturbation (before and after), and Trigger (self- and experimenter-triggered). The main effect of Time was significant on  $\Delta V_{Fn}$  and  $\Delta V_M$  ( $F_{1,14} = 10.75$ ,  $p < .01$  for  $\Delta V_{Fn}$ ;  $F_{1,14} = 10.81$ ,  $p < .01$  for  $\Delta V_M$ ) with a significant Time  $\times$  Group interaction ( $F_{1,14} = 5.17$ ,  $p < .05$  for  $\Delta V_{Fn}$ ;  $F_{1,14} = 4.98$ ,  $p < .05$  for  $\Delta V_M$ ). The significant Time  $\times$  Group interactions on  $\Delta V_{Fn}$  and  $\Delta V_M$  were caused by the fact that  $\Delta V$  differences between 0 and 6 wk. were significant in the wrist training group only, which was confirmed by *post*

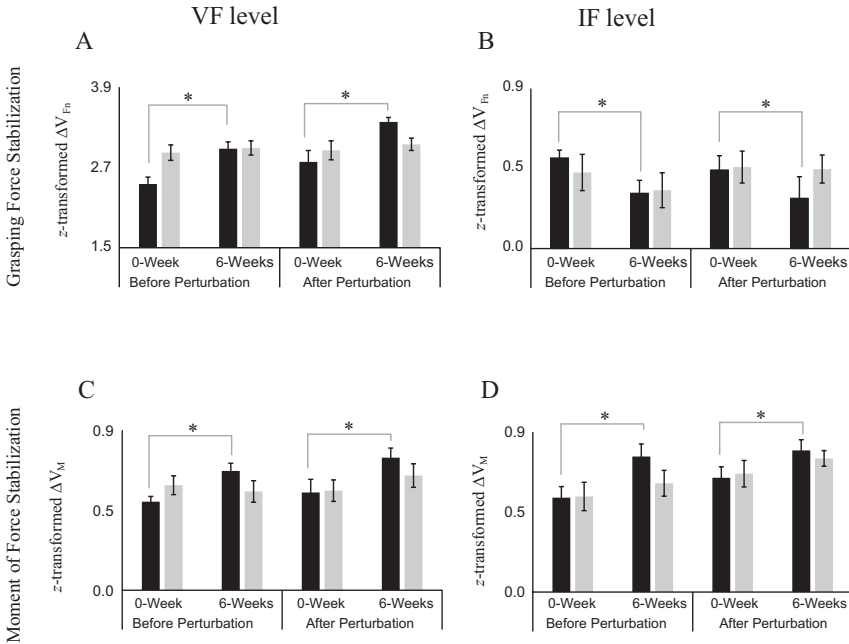


FIG. 4. z-transformed  $\Delta V$  (dimensionless) for grasping force ( $F_N$ ) and moment of force ( $M_{TOT}$ ) at the VF and IF level analyses. Black bars (wrist training group) and grey bars (control group) represent  $\Delta V$ . Average  $\Delta V_z$  across participants are presented with standard error bars. \* $p < .05$ .

*hoc* comparisons ( $p < .05$ ). The main effect of Perturbation was significant only on  $\Delta V_M$  without an interaction ( $F_{1,14} = 5.22, p < .05$ ).

*Anticipatory Synergy Adjustment*

The time of anticipatory synergy adjustment ( $t_{ASA}$ ) was quantified, which represents the time of initiation of changes in  $\Delta V_z$  prior to the time of initiation of the perturbation ( $t_0$ ). Overall, an early change in  $\Delta V_z$  with respect to  $t_0$  was observed in both wrist training and control group participants at the self-triggered condition (on average, by about 130 msec.). Furthermore, anticipatory synergy adjustments in the self-triggered condition were observed in both upper (virtual finger level) and lower (individual finger level) analysis. However, the early change in  $\Delta V_z$  prior to  $t_0$  was not clearly seen in the experimenter-triggered condition where the participant did not know the timing information of upcoming perturbation (Fig. 5).

There was no significant difference between the magnitude of  $t_{ASA}$  of  $\Delta V_{F_N}$  (grasping force stabilization) and  $\Delta V_M$  (moment of force stabilization) in the self-triggered condition ( $p > .05$ ). In addition, significant differ-

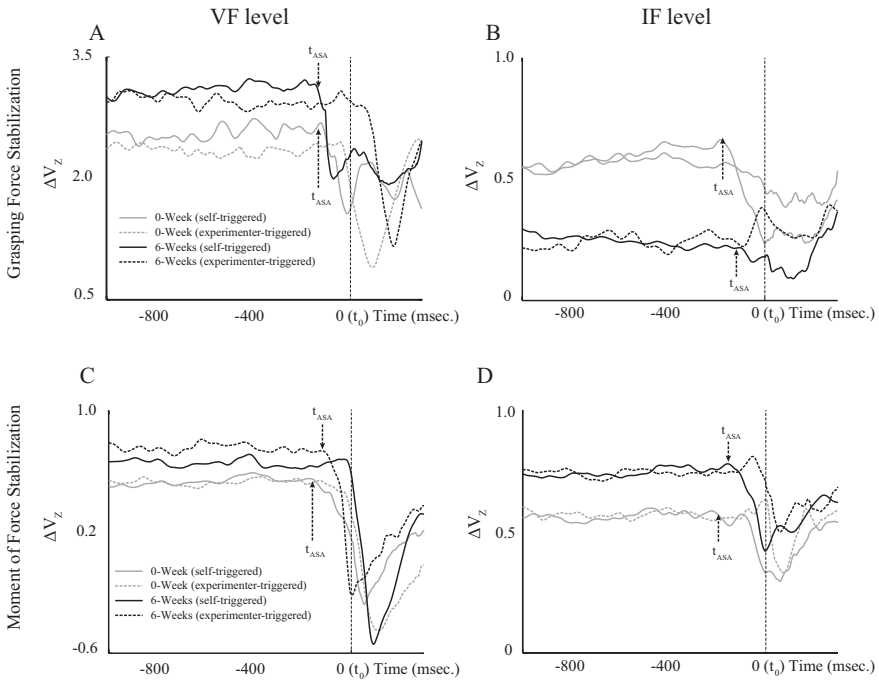


FIG. 5.  $z$ -transformed  $\Delta V$  of the grasping force and moment of force at the virtual finger (VF) level (A and C) and individual finger (IF) level (B and D). Averages across participants in the wrist training group are presented for  $\Delta V_z$ . The times of anticipatory synergy adjustment ( $t_{ASA}$ ) are indicated with arrows.

ence of  $t_{ASA}$  between 0 and 6 wk. was not observed in  $t_{ASA}$  of both  $\Delta V_{FH}$  and  $\Delta V_M$  ( $p > .05$ ), which implies no training effect on  $t_{ASA}$ .

## DISCUSSION

The two hypotheses formulated in the Introduction were supported by the data. It was observed that the wrist strengths and the synergy indices of both digit force- and moment-stabilization at the steady-state increased with 6 wk. of wrist strength training, in support of Hypothesis 1. There was no significant change in the time of anticipatory synergy adjustment ( $t_{ASA}$ ) after training, which supports the second hypothesis. The following sections will focus on the possible mechanism of neuromuscular adaptation with strength training during the multi-digit prehension tasks.

### *Changes in Multi-digit Coordination with Strength Training*

Earlier studies have shown that finger coordination improves with task-specific practice of finger strength training (Dons, Bollerup, Bond-Petersen, & Hancke, 1979; Sale, 1987; Enoka, 1997; Shim, *et al.*, 2008). These

studies support the claim that strength training is important not only for gaining higher force production capability but also for enhancing neural organization or neuromuscular adaptation during motor tasks (Enoka, 1988). In the current study, the presence of synergy (i.e.,  $\Delta V > 0$ ) was observed in both grasping force ( $F_N$ ) and moment of force ( $M_{TOT}$ ) at the virtual finger level, and its strength (i.e., the magnitude of synergy index) increased with 6 wk. of the wrist strength training (Fig. 4A and 4C). However, there was no significant training effect on the synergy indices of tangential force ( $F_T$ ). The performance variables at the virtual finger level directly describe the two important controls (i.e., grasping and rotational equilibrium controls) taken with a hand-held object; therefore, the stabilization of apparent performance variables, which are affected and coordinated by the virtual finger level of variables, is critical to ensure a stable performance of prehensile action. The actions of individual fingers are coordinated to generate desired task-specific outcomes of the virtual finger actions (Flanders & Soechting, 1995; Yoshikawa, 1999; Baud-Bovy & Soechting, 2001; Shim, Latash, & Zatsiorsky, 2005a); therefore, the stabilization of the performance is not directly affected by the stabilization (or destabilization) of variables at the individual finger level. Note that the desired values in the upper hierarchy (e.g., the virtual finger and thumb forces and moments), which satisfy the task mechanics, do not necessarily need to specify a unique combination of the lower level variables (e.g., individual finger forces and moments) in the redundant system.

The current results indicated that the resistance training on the wrist could be an effective way to enhance the ability to organize end-effector forces (by neuromuscular adaptation at a neural level) exclusively at the upper level variables during multi-digit grasping tasks along with gaining voluntary muscle force production (by muscle hypertrophy at a peripheral level). It is of interest how the synergy indices change with the wrist strength training. A model with a two-level hierarchy has been proposed to describe the control of hand/finger actions (Arbib, Iberall, & Lyons, 1985; MacKenzie & Iberall, 1994), and this model could explain the effect of strength training on synergic actions of the hand digits. The mechanically necessitated couplings among variables either at the individual or at the virtual finger levels have been explained using chain effects (Gregory, 2002; Zatsiorsky, Gao, & Latash, 2003b; Shim, *et al.*, 2005a). Furthermore, Gorniak, Zatsiorsky, & Latash (2009) proposed another line of chain effect (so-called synergic chain effect) to address logical relations of "good" and "bad" variances at the upper and lower level of synergies. In the current study, grasping force stabilizing synergy was observed in the upper level (virtual finger level) only, whereas moment of force stabilizing synergies were present at both levels of synergy hierarchies.



Figure 6 illustrates a simple case of three digit (two fingers and thumb) grasping tasks, which could describe  $\Delta V$  changes with training in the current study. As depicted in Fig. 6, the grasping force synergy increases with training at the virtual finger level by increasing good variance ( $V_{GOOD}$ ) and decreasing bad variance ( $V_{BAD}$ ), which is similar to the patterns of changes in the two variances with practice (Wu, Pazin, Zatsiorsky, & Latash, 2012). An increase in  $V_{GOOD}$  at the virtual finger level after training should be associated with an increase in  $V_{BAD}$  at the individual finger level because the virtual finger grasping forces are the performance variables of individual finger grasping force actions (i.e., sum of individual finger grasping forces = virtual finger grasping force) and the magnitude of  $V_{BAD}$  of individual finger forces coordination is determined by the magnitude of variance in the performance variables (i.e.,  $V_{BAD}$  at the individual finger level affects the performance variable, virtual finger grasping force). In other words, the participants performed the grasping actions in more flexible ways (larger  $V_{GOOD}$  at the virtual finger level) with reduced performance errors (smaller  $V_{BAD}$  at the virtual finger level) after training, which ensured a stable grasping action with training.

An increase in  $V_{BAD}$  at the individual finger level reflects that positive co-variation among individual finger grasping forces was stronger following the wrist strength training. The positive co-variation between individual finger forces resulted from finger force changes in the same direction, which hampered error compensation among the fingers for resultant grasping force production. It has been revealed in studies with strength training that individual finger actions were less independent with higher maximal voluntary force magnitude (Olafsdottir, *et al.*, 2008; Shim, *et al.*, 2008). Consequently, less individuated finger actions following training encourage a strong positive co-variation of individual finger grasping forces. In other words, a strong positive co-variation of finger grasping forces after training, which was possibly due to less independent actions of fingers after training, seemingly caused a detrimental effect in performing the tasks at the individual finger level (i.e., increased  $V_{BAD}$ ). However, the synergy of the grasping force stabilization at the upper level shows a significant increase after training, meaning that less dexterous (independent) actions in lower level variables could lead to positive consequence in upper level variables after training in the multi-digit prehension tasks.

For  $M_{TOT}$  stabilization, the synergic action ( $\Delta V > 0$ ) was observed in both virtual and individual finger level analysis, and the strength of the synergy increased with training. After training, both  $V_{GOOD}$  and  $V_{BAD}$  decreased at the virtual finger level while the rate of  $V_{BAD}$  decrease was larger than that of  $V_{GOOD}$  decrease, resulting in a  $\Delta V$  increase after training. The decreased  $V_{GOOD}$  at the virtual finger level brought corresponding changes in  $V_{BAD}$  at

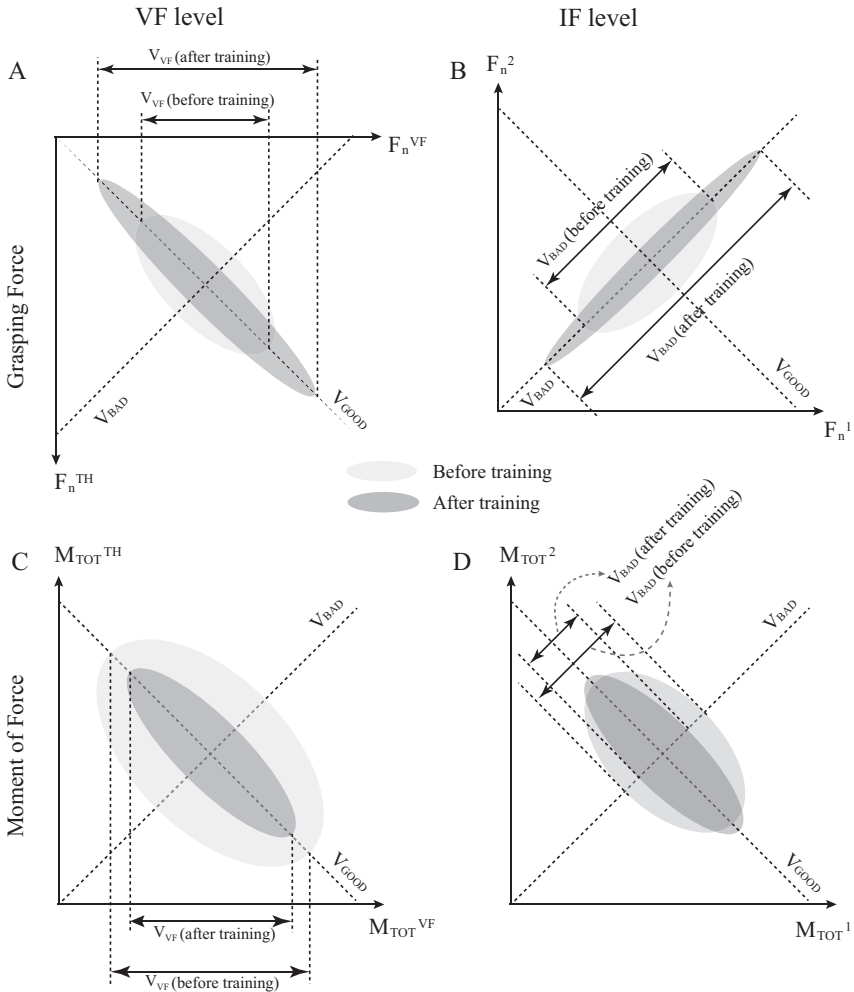


FIG. 6. An illustration of changes in two sources of variability ( $V_{GOOD}$  and  $V_{BAD}$ ) in three tasks requiring digit grasping force and moment of force production. Grasping force variability at (A) the virtual finger (VF) level and (B) individual finger (IF) level. Moment of force variability at (C) the virtual finger level (VF) and (D) the individual finger (IF) level.

the individual finger level (i.e., decreased  $V_{BAD}$  at the individual finger level in Fig. 6C and 6D).  $V_{BAD}$  also decreased at the individual finger level; hence, the synergy of  $M_{TOT}$  exists at both levels and its strength increases with wrist strength training. Thus, the current study indicates that neuromuscular training induces a parallel improvement in both strength of forearm/hand and indices of stability in grasping action (i.e., grasping force and moment stability) at the upper hierarchy of static prehension control.

The patterns of data distribution in redundant motor systems have been described by several neural mechanisms including the central-back-coupling model (Latash, Shim, Smilga, & Zatsiorsky, 2005), the optimal feedback control model (Todorov & Jordan, 2002), the feed-forward model (Goodman & Latash, 2006), and the referent configuration hypothesis in a hierarchical control system (Ostry & Feldman, 2003; Pilon, De Serres, & Feldman, 2007; Feldman, 2008). The training effect in synergy indices of the performance variables and patterns of element interactions in the current study could be incorporated with the central-back-coupling model. The model proposes the idea that the bifurcated control variables were involved in the redundant system (Latash, *et al.*, 2005). One variable defined a desired trajectory of salient performance variables at the upper level (i.e., performance variables at the virtual finger level in the current study), and an average sharing pattern of elemental variables which was possibly relevant to an optimization function (Park, Zatsiorsky, & Latash, 2010; Park, Sun, Zatsiorsky, & Latash, 2011). The other variable in the central-back-coupling model was consistent with patterns of element interactions such as co-variation of elemental variables, which are associated with the stabilization of virtual finger variables. The model is able to interpret the changes in the pattern of data distribution after training in the current study, which showed the stabilization of two important performance variables (grasping force and resultant moment of force) and its improvement with training explicitly at the upper level where the apparent stabilization of prehensile action was described.

#### *Anticipatory Synergy Adjustment*

It was expected that the ability to adjust synergies in a feed-forward manner in preparation to an upcoming perturbation (i.e., anticipatory synergy adjustment) would not improve after strength training in the self-triggered condition. It has been assumed that anticipatory synergy adjustments affect the neural variables that are incorporated into stability properties of performance variables. The ability for anticipation is weakened by the aging process (Olafsdottir, *et al.*, 2007) or by malfunctioning of the sub-cortical loop (Park, *et al.*, 2012, 2013). Thus, it was suggested that the synergic actions of elemental variables and their feed-forward adjustment in the redundant system is the function of subcortical structures including basal ganglia and the cerebellum.

By combining the aforementioned studies with the elderly and patients with sub-cortical disorder, one may assume that the strength of anticipatory synergy adjustments correlates with strength of hand/finger since the groups of elderly and patients had lower hand/finger strength. However, the significant deficits in anticipatory synergy adjustments and force stabilization synergies were reported in the study with a normal

group with vibration treatment on extrinsic and intrinsic hand muscles, while no significant change in maximal voluntary finger forces (Arpinar-Avsar, Park, Zatsiorsky, & Latash, 2013). The deficit in anticipatory synergy adjustment may reflect supraspinal effects of the vibration-induced afferent activity (e.g., interaction with cortico-basal-thalamo-cortical loops); therefore, central control signals in feed-forward adjustment may not be mediated by change in strength at a peripheral level.

However, it is possible that there may not be much room to improve the ability of anticipatory synergy adjustments since the training effects on the maximal voluntary torque in supination and pronation directions, which were the same as the direction of torque perturbation, were weaker than the effects in other directional torques. That is, the most obvious problem of the current training device was the “lack of external torque” at the neutral position. In particular, during a pronation-supination exercise as shown in Fig. 1A, the external/resistant torque at the neutral position was close to zero because the moment arm at the neutral position was close to zero. Hence, the training effect may not be strong enough to encourage significant changes in anticipatory synergy adjustments. It should be acknowledged that the direction of torque perturbation was limited to supination only, so the full effect of training on anticipatory synergy adjustments is still in question. Also, the current task and analysis were limited to the two-dimensional planar grasping and its subset constraints. Since natural prehensile actions (e.g., grasping and rotational actions) are observed in a three-dimensional space, the conjoint change of digit coordination in a three-dimensional space against various directional external torques and its training effect remain to be explored.

Finally, the results of the current study encourage further investigations of the strength training effect on hand/digit coordination during everyday activities (i.e., handwriting, keyboard typing, handling many hand-held objects including tray, tablet computer, etc.) in elderly individuals, which would not only provide insight for understanding the aging process but also offer ideas of evidence-based interventions for slowing or “reversing” the adverse consequences of aging.

#### REFERENCES

- ARBIB, M. A., IBERALL, T., & LYONS, D. (1985) Coordinated control programs for movements of the hand. In A. W. Goodwin & I. Darian-Smith (Eds.), *Hand function and the neocortex*. Berlin, Germany: Springer-Verlag. Pp. 111-129.
- ARPINAR-AVSAR, P., PARK, J., ZATSIORSKY, V. M., & LATASH, M. L. (2013) Effects of muscle vibration on multi-finger interaction and coordination. *Experimental Brain Research*, 229(1), 103-111.
- BAUD-BOVY, G., & SOECHTING, J. F. (2001) Two virtual fingers in the control of the tripod grasp. *Journal of Neurophysiology*, 86(2), 604-615.

- BILODEAU, M., KEEN, D. A., SWEENEY, P. J., SHIELDS, R. W., & ENOKA, R. M. (2000) Strength training can improve steadiness in persons with essential tremor. *Muscle Nerve*, 23(5), 771-778.
- BRYLINSKYL, J., MOORE, J. C., & FROSCHE, M. (1992) The effect of using a weighted softball on pitching velocity, wrist strength and handgrip. *Journal of Strength and Conditioning Research*, 6(3), 170-173.
- DANION, F., SCHONER, G., LATASH, M. L., LI, S., SCHOLZ, J. P., & ZATSORSKY, V. M. (2003) A mode hypothesis for finger interaction during multi-finger force-production tasks. *Biological Cybernetics*, 88(2), 91-98.
- DELIS, I., BERRET, B., POZZO, T., & PANZERI, S. (2013) Quantitative evaluation of muscle synergy models: a single-trial task decoding approach. *Frontiers in Computational Neuroscience*, 7, 8.
- DONS, B., BOLLERUP, K., BONDE-PETERSEN, F., & HANCKE, S. (1979) The effect of weightlifting exercise related to muscle fiber composition and muscle cross-sectional area in humans. *European Journal of Applied Physiology and Occupational Physiology*, 40, 95-106.
- ENOKA, R. M. (1988) Muscle strength and its development. *Sports Medicine*, 6(3), 146-168.
- ENOKA, R. M. (1997) Neural strategies in the control of muscle force. *Muscle Nerve*, 5(Suppl.), S66-S69.
- FELDMAN, A. G. (2008) Threshold position control signifies a common spatial frame of reference for motor action and kinesthesia. *Brain Research Bulletin*, 75(5), 497-499.
- FLANDERS, M., & SOECHTING, J. F. (1995) Frames of reference for hand orientation. *Journal of Cognitive Neuroscience*, 7(2), 182-195.
- FRIEDMAN, J., SKM, V., ZATSORSKY, V. M., & LATASH, M. L. (2009) The sources of two components of variance: an example of multifinger cyclic force production tasks at different frequencies. *Experimental Brain Research*, 196(2), 263-277.
- GELFAND, I. M., & LATASH, M. L. (1998) On the problem of adequate language in motor control. *Motor Control*, 2(4), 306-313.
- GOODMAN, S. R., & LATASH, M. L. (2006) Feed-forward control of a redundant motor system. *Biological Cybernetics*, 95(3), 271-280.
- GORNIK, S. L., ZATSORSKY, V. M., & LATASH, M. L. (2009) Hierarchical control of static prehension: II. Multi-digit synergies. *Experimental Brain Research*, 194(1), 1-15.
- GREGORY, R. W. (2002) *Biomechanics and control of force and torque production in multi-finger prehension*. State College, PA: The Pennsylvania State Univer.
- HAZELTON, F. T., SMIDT, G. L., FLATT, A. E., & STEPHENS, R. I. (1975) The influence of wrist position on the force produced by the finger flexors. *Journal of Biomechanics*, 8(5), 301-306.
- HORII, E., LIN, G. T., COONEY, W. P., LINSCHIED, R. L., & AN, K. N. (1992) Comparative flexor tendon excursion after passive mobilization: an in vitro study. *The Journal of Hand Surgery*, 17(3), 559-566.
- IMRHAN, S. N., & LOO, C. H. (1988) Modelling wrist-twisting strength of the elderly. *Ergonomics*, 31(12), 1807-1819.
- KANG, N., SHINOHARA, M., ZATSORSKY, V. M., & LATASH, M. L. (2004) Learning multi-finger synergies: an uncontrolled manifold analysis. *Experimental Brain Research*, 157(3), 336-350.
- KEOGH, J. W., MORRISON, S., & BARRETT, R. (2007) Strength training improves the tri-digit finger-pinch force control of older adults. *Archives of Physical Medicine Rehabilitation*, 88(8), 1055-1063.
- LATASH, M. L. (2012) The bliss (not the problem) of motor abundance (not redundancy). *Experimental Brain Research*, 217(1), 1-5.

- LATASH, M. L., SCHOLZ, J. P., & SCHONER, G. (2002) Motor control strategies revealed in the structure of motor variability. *Exercise and Sport Sciences Review*, 30(1), 26-31.
- LATASH, M. L., SHIM, J. K., SMILGA, A. V., & ZATSIORSKY, V. M. (2005) A central back-coupling hypothesis on the organization of motor synergies: a physical metaphor and a neural model. *Biological Cybernetics*, 92(3), 186-191.
- LEDEBT, A., BRIL, B., & BRENIERE, Y. (1998) The build-up of anticipatory behaviour: an analysis of the development of gait initiation in children. *Experimental Brain Research*, 120(1), 9-17.
- MACKENZIE, C. L., & IBERALL, T. (1994) *The grasping hand*. Amsterdam, The Netherlands: Elsevier Science B.V.
- O'DRISCOLL, S. W., HORII, E., NESS, R., CAHALAN, T. D., RICHARDS, R. R., & AN, K. N. (1992) The relationship between wrist position, grasp size, and grip strength. *The Journal of Hand Surgery*, 17(1), 169-177.
- OLAFSDOTTIR, H. B., YOSHIDA, N., ZATSIORSKY, V. M., & LATASH, M. L. (2005) Anticipatory covariation of finger forces during self-paced and reaction time force production. *Neuroscience Letters*, 381(1-2), 92-96.
- OLAFSDOTTIR, H. B., YOSHIDA, N., ZATSIORSKY, V. M., & LATASH, M. L. (2007) Elderly show decreased adjustments of motor synergies in preparation to action. *Clinical Biomechanics (Bristol, Avon)*, 22(1), 44-51.
- OLAFSDOTTIR, H. B., ZATSIORSKY, V. M., & LATASH, M. L. (2008) The effects of strength training on finger strength and hand dexterity in healthy elderly individuals. *Journal of Applied Physiology*, 105(4), 1166-1178.
- OLDFIELD, R. C. (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9, 97-113.
- OSTRY, D. J., & FELDMAN, A. G. (2003) A critical evaluation of the force control hypothesis in motor control. *Experimental Brain Research*, 153(3), 275-288.
- PARK, J., LEWIS, M. M., HUANG, X., & LATASH, M. L. (2013) Effects of olivo-ponto-cerebellar atrophy (OPCA) on finger interaction and coordination. *Clinical Neurophysiology*, 124(5), 991-998.
- PARK, J., SUN, Y., ZATSIORSKY, V. M., & LATASH, M. L. (2011) Age-related changes in optimality and motor variability: an example of multifinger redundant tasks. *Experimental Brain Research*, 212(1), 1-18.
- PARK, J., WU, Y. H., LEWIS, M. M., HUANG, X., & LATASH, M. L. (2012) Changes in multifinger interaction and coordination in Parkinson's disease. *Journal of Neurophysiology*, 108(3), 915-924.
- PARK, J., ZATSIORSKY, V. M., & LATASH, M. L. (2010) Optimality vs. variability: an example of multi-finger redundant tasks. *Experimental Brain Research*, 207(1-2), 119-132.
- PILON, J. F., DE SERRES, S. J., & FELDMAN, A. G. (2007) Threshold position control of arm movement with anticipatory increase in grip force. *Experimental Brain Research*, 181(1), 49-67.
- REILLY, K. T., & HAMMOND, G. R. (2000) Independence of force production by digits of the human hand. *Neuroscience Letter*, 290(1), 53-56.
- SALE, D. G. (1987) Influence of exercise and training on motor unit activation. *Exercise and Sport Sciences Reviews*, 15, 95-151.
- SCHOLZ, J. P., KANG, N., PATTERSON, D., & LATASH, M. L. (2003) Uncontrolled manifold analysis of single trials during multi-finger force production by persons with and without Down syndrome. *Experimental Brain Research*, 153(1), 45-58.

- SCHOLZ, J. P., & SCHONER, G. (1999) The uncontrolled manifold concept: identifying control variables for a functional task. *Experimental Brain Research*, 126(3), 289-306.
- SHIM, J. K., HSU, J., KAROL, S., & HURLEY, B. F. (2008) Strength training increases training-specific multifinger coordination in humans. *Motor Control*, 12(4), 311-329.
- SHIM, J. K., LATASH, M. L., & ZATSIORSKY, V. M. (2003) Prehension synergies: trial-to-trial variability and hierarchical organization of stable performance. *Experimental Brain Research*, 152(2), 173-184.
- SHIM, J. K., LATASH, M. L., & ZATSIORSKY, V. M. (2005a) Prehension synergies in three dimensions. *Journal of Neurophysiology*, 93(2), 766-776.
- SHIM, J. K., LATASH, M. L., & ZATSIORSKY, V. M. (2005b) Prehension synergies: trial-to-trial variability and principle of superposition during static prehension in three dimensions. *Journal of Neurophysiology*, 93(6), 3649-3658.
- SHIM, J. K., & PARK, J. (2007) Prehension synergies: principle of superposition and hierarchical organization in circular object prehension. *Experimental Brain Research*, 180(3), 541-556.
- SHIM, J. K., PARK, J., ZATSIORSKY, V. M., & LATASH, M. L. (2006) Adjustments of prehension synergies in response to self-triggered and experimenter-triggered load and torque perturbations. *Experimental Brain Research*, 175(4), 641-653.
- SU, F. C., CHOU, Y. L., YANG, C. S., LIN, G. T., & AN, K. N. (2005) Movement of finger joints induced by synergistic wrist motion. *Clinical Biomechanics (Bristol, Avon)*, 20(5), 491-497.
- THORSEN, R. A., OCCHI, E., BOCCARDI, S., & FERRARIN, M. (2006) Functional electrical stimulation reinforced tenodesis effect controlled by myoelectric activity from wrist extensors. *Journal of Rehabilitation and Research Development*, 43(2), 247-256.
- TODOROV, E., & JORDAN, M. I. (2002) Optimal feedback control as a theory of motor coordination. *Nature Neuroscience*, 5(11), 1226-1235.
- WU, Y. H., PAZIN, N., ZATSIORSKY, V. M., & LATASH, M. L. (2012) Practicing elements versus practicing coordination: changes in the structure of variance. *Journal of Motor Behavior*, 44(6), 471-478.
- YOSHIKAWA, T. (1999) Virtual Truss model for characterization of internal forces for multiple finger grasps. *IEEE Transactions on Robotic Automation*, 15(5), 941-947.
- ZATSIORSKY, V. M., GAO, F., & LATASH, M. L. (2003a) Finger force vectors in multi-finger prehension. *Journal of Biomechanics*, 36(11), 1745-1749.
- ZATSIORSKY, V. M., GAO, F., & LATASH, M. L. (2003b) Prehension synergies: effects of object geometry and prescribed torques. *Experimental Brain Research*, 148(1), 77-87.
- ZATSIORSKY, V. M., LATASH, M. L., GAO, F., & SHIM, J. K. (2004) The principle of superposition in human prehension. *Robotica*, 22(2), 231-234.
- ZATSIORSKY, V. M., LI, Z. M., & LATASH, M. L. (2000) Enslaving effects in multi-finger force production. *Experimental Brain Research*, 131(2), 187-195.
- ZHOU, T., WU, Y. H., BARTSCH, A., CUADRA, C., ZATSIORSKY, V. M., & LATASH, M. L. (2013) Anticipatory synergy adjustments: preparing a quick action in an unknown direction. *Experimental Brain Research*, 226(4), 565-573.
- ZHANG, W., SAINBURG, R. L., ZATSIORSKY, V. M., & LATASH, M. L. (2006) Hand dominance and multi-finger synergies. *Neuroscience Letters*, 409(3), 200-204.

## APPENDIX

*Uncontrolled Manifold Analysis*

(see Scholz & Shoner, 1999; Latash, et al., 2002, for details)

The uncontrolled manifold analysis was performed for each performance variable ( $F_N$ ,  $F_T$ , and  $M_{TOT}$ ) at each level of analysis (e.g., individual and virtual finger levels).

*Individual Finger Level Analysis*

For  $F_N^{VF}$ , changes in the normal forces of individual fingers sum up to produce a change in  $F_N^{VF}$ :

$$dF_N^{VF} = [ 1 \ 1 \ 1 \ 1 ] \cdot [ dF_N^I \ dF_N^M \ dF_N^R \ dF_N^L ]^T \quad (A1)$$

The uncontrolled manifold was defined as an orthogonal set of the vectors  $e_i$  in the space of the individual finger forces that did not change the averaged  $F_N^{VF}$  across trials:

$$0 = [ 1 \ 1 \ 1 \ 1 ] \cdot e_i \quad (A2)$$

These directions were found by computing the null-space of the Jacobian of this transformation ( $[ 1 \ 1 \ 1 \ 1 ] \cdot e_i$ ). The mean-free forces were then projected onto these directions and summed to produce:

$$f_{||} = \sum_i^{n-p} (e_i^T \cdot df) \cdot e_i \quad (A3)$$

where ' $n=4$ ', which corresponds to the number of degrees-of-freedom of the elemental variables, and ' $p=1$ ', which is the number of degrees-of-freedom of the performance variable ( $F_N^{VF}$ ). The component of the de-measured forces orthogonal to the null-space is given by:

$$f_{\perp} = df - f_{||} \quad (A4)$$

The amount of variance per degree of freedom parallel to the uncontrolled manifold space is computed by:

$$V_{UCM} = \frac{\sum |f_{||}|^2}{(n-p) \cdot N_{trials}} \quad (A5)$$

The amount of variance per degree of freedom orthogonal to the uncontrolled manifold is:

$$V_{ORT} = \frac{\sum |f_{\perp}|^2}{p \cdot N_{trials}} \quad (A6)$$

The normalized difference between these variances is quantified by a variable  $\Delta V$ :

$$\Delta V = \frac{V_{UCM} - V_{ORT}}{V_{TOT}} \quad (A7)$$



where  $V_{TOT}$  stands for the total variance per degree of freedom. Note that positive  $\Delta V$  (i.e.,  $V_{UCM} > V_{ORT}$ ) was caused by dominant negative co-variation of the individual finger forces, which the authors interpret as evidence for a force-stabilizing synergy. In contrast,  $\Delta V=0$  indicates independent variation of the finger forces, while  $\Delta V < 0$  indicates positive co-variation of the individual finger forces, which contributes to variance of  $F_N^{VF}$ .

A similar procedure was used to compute the two variance components related to stabilization of  $F_T^{VF}$  and  $M^{VF}$  as performance variables.

#### *Virtual Finger Level Analysis*

For the uncontrolled manifold analysis at the virtual finger level, three performance variables were  $F_N^{TOT}$ ,  $F_T^{TOT}$ , and  $M^{TOT}$ . The elemental variables were the thumb and virtual finger components of forces and moment. The computational steps were the same as the uncontrolled manifold analysis at the individual finger level, while the Jacobian at the virtual finger level analysis was  $\begin{bmatrix} 1 & 1 \end{bmatrix}$  because two elements of the thumb and virtual finger variables were considered in the virtual finger level analysis. The dimensionalities of  $V_{UCM}$  and  $V_{ORT}$  with respect to three performance variables were a value of one for each.