Exp Brain Res (2007) 180:541–556
DOI 10.1007/s00221-007-0872-9

RESEARCH ARTICLE

Prehension synergies: principle of superposition and hierarchical organization in circular object prehension

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Received: 4 October 2006 / Accepted: 11 January 2007 / Published online: 6 February 2007

Abstract This study tests the following hypotheses in multi-digit circular object prehension: the principle of superposition (i.e., a complex action can be decomposed into independently controlled sub-actions) and the hierarchical organization (i.e., individual fingers at the lower level are coordinated to generate a desired task-specific outcome of the virtual finger at the higher level). Subjects performed 25 trials while statically holding a circular handle instrumented with five six-component force/moment sensors under seven external torque conditions. We performed a principal component (PC) analysis on forces and moments of the thumb and virtual finger (VF: an imagined finger producing the same mechanical effects of all finger forces and moments combined) to test the applicability of the principle of superposition in a circular object prehension. The synergy indices, measuring synergic actions of the individual finger (IF) moments for the stabilization of the VF moment, were calculated to test the hierarchical organization. Mixed-effect ANOVAs were used to test the dependent variable differences for different external torque conditions and different fingers at the VF and IF levels. The PC analysis showed that the elemental variables were decoupled into two groups: one group related to grasping stability control (normal force control) and the other group associated with rotational equilibrium control (tangential force control), which supports the principle of superposition. The synergy indices were always positive, suggesting error compensations between IF moments for the VF moment stabilization, which confirms the hierarchical organization of multi-digit prehension.

Keywords Finger · Virtual finger · Circular object · Principle of superposition · Hierarchical control · Variability · UCM

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Introduction

Everyday motor tasks demand the central nervous system (CNS) to be capable of coordinating multiple effectors involved in achieving the task objectives. This often requires the CNS to govern more effectors than are minimally necessary. This problem has been known as the 'motor redundancy/abundance' (Bernstein 1935, 1967; Turvey 1990; Latash 2000). Multi-digit prehension is performed by a kinetically redundant system, e.g., there are typically more digits involved in the process of turning a door knob or holding a glass of water than the two digits which are minimally required. The redundant hand system allows an infinite number of solutions for a same prehension task (Santello and Soechting 2000; Zatsiorsky et al. 2003; Shim et al. 2005a, 2006c). Thus, the central nervous system (CNS) needs to decide what specific solution(s) of forces and moments of force to be used to solve the redundancy problem. Previous studies have suggested that the CNS solves the problem of motor redundancy not by having one specific solution but by allowing a family of solutions that satisfy task requirements (Gelfand and Tsetlin 1966; Scholz and Schoner 1999; d'Avella et al. 2003; Shim et al. 2004c, 2005b; Latash et al. 2005a).

Recent studies on multi-digit prehension of rectangular objects employed trial-to-trial variability analysis and provided evidences of two independent groups of mechanical variables in static prehension (Shim et al. 2003b, 2005a; Zatsiorsky et al. 2004): one group contains grasping forces (normal forces) that are related to the ''stability of grasping'' and the other group includes load forces (tangential forces) and moments of normal and tangential forces that are associated with the ''rotational equilibrium'' of the hand-held object. This claim was made by showing coupling of variables in each group and decoupling of variables between the two groups. This type of decoupled control was first suggested in robotics and called the 'principle of superposition' (Arimoto and Nguyen 2001; Arimoto et al. 2001; Doulgeri et al. 2002). According to the principle of superposition, some sub-actions (e.g., grasping a hand-held object and rotating the object) can be controlled by independent control processes and the total processing/computation time can be reduced by employing this strategy. The present context of grasping stability has been limited to slip prevention.

Although previous experiments showed that the principle of superposition was also supported in static human prehension (Shim et al. 2003b, 2005a; Zatsiorsky et al. 2004), the geometry of the hand-held objects used in the previous experiments was limited to a 'rectangular/parallelepiped shape' which necessitates the coupling of grasping forces (e.g., the grasping forces of a thumb and fingers should cancel out to be zero) and the coupling of load forces and moments of forces (e.g., the sum of the load forces of all digits should cancel out the weight of a grasping object). Due to the pre-imposed relationship between the mechanical variables during prehension of a rectangular object, the generalizability of the principle of superposition is currently questionable for prehension of objects in other geometric shapes which do necessitate the coupling of mechanical variables. Here an interesting question arises. Will the principle of superposition still be valid when grasping force of the thumb (e.g., the thumb normal force) and the grasping force of individual fingers (e.g., the sum of individual finger normal forces) are not mechanically coupled?

In this study we used a circular object to study the generalizability of the principle of superposition because prehension of a circular object presents a geometry in which the scalar sum of the individual finger (IF) normal forces [defined as the virtual finger (VF) normal force] is not necessarily required to be the same as the thumb normal force. In prehension of a circular object, therefore, it is not clear whether the thumb and VF normal forces would even form a group of coupled variables. If the CNS controls the thumb and VF normal forces using one command regardless of the geometry of the hand-held objects, we may expect to find a coupling of thumb and VF normal forces and a decoupling of normal and tangential forces during circular object prehension, thus supporting the generalizability of the principle of superposition in a circular object prehension.

Previous theoretical studies (Cutkosky and Howe 1990; Iberall 1997; Yoshikawa 1999) as well as experimental studies on hand and finger actions (Santello and Soechting 1997; Baud-Bovy and Soechting 2001; Shim et al. 2003b, 2005a) have suggested a hierarchical control of multi-digit prehension based on the notions of the VF and IF, i.e., at the higher level (VF level) the thumb and VF are coordinated to satisfy task mechanics whereas at the lower level (IF level) the individual fingers are coordinated to generate a desired task-specific outcome of the virtual finger during multi-digit manipulation tasks. Previous studies on multi-digit pressing (Li et al. 1998; Shinohara et al. 2003) and all-digit rectangular object prehension (Shim et al. 2004c, 2005b, 2006c) used the indices of covariation (ΔVar and ΔVar_{norm}; these variables are similar to negated covariations between elemental variables; see Methods for computational details) between finger forces and moments of force, and showed that the CNS makes fine adjustments of IF forces/moments at the lower level to stabilize VF forces/moments at the higher level. Both multi-digit pressing and multi-digit prehension of a rectangular object offer parallel actions of fingers. Therefore, it is currently unknown whether the hierarchical control hypothesis is valid for other multi-digit manipulation tasks, especially for a task encouraging non-parallel actions of fingers such as multi-digit prehension of a circular object.

We asked subjects to statically hold a circular handle multiple times under systematically varied external torques and recorded forces and moments of force at each digit contact. Although the terms 'torque' and 'moment of force' are used interchangeably in mechanics, in this paper we will use 'torque' to designate the external torque (the rotational force externally imposed by locating a load at different positions; see Methods for details) and use 'moment of force' or 'moment' to signify a rotational force produced by a subject to overcome the external torque during static prehension. We analyzed intra-subject trial-to-trial variability of forces and moments of force produced by hand digits. This approach is based on the idea that the

CNS prefers a family of solutions rather than one specific solution for a redundant motor task. Thus, studying a family of solutions recorded from multiple trials for the same motor task may reveal the strategies used by the CNS to resolve the motor redundancy. The previous work as well as the theoretical position, which support the idea that the strategies utilized by the CNS in multi-digit grasping should be invariant to tasks, leads the hypothesis that the principle of superposition and the hierarchical organization of multi-digit control are also valid in circular object prehension task.

Methods

Subjects

Eight right-handed males participated in this study as subjects (age: 27.3 ± 2.7 years, weight: 70.9 ± 3.8, height: 177.2 ± 5.1 cm, hand length: 20.1 ± 2.2 cm, and hand width: 9.0 ± 2.7). The hand lengths were measured between the distal crease of the wrist and the middle finger tip when a subject positioned the palm side of the right hand and the lower arm on a table with all finger joints extended. The hand width was measured between the radial side of the index finger metacarpal joint and the ulnar side of the little finger metacarpal joint. All subjects gave informed consent according to the protocol approved by the University of Maryland after the purpose and the involved experimental procedures of the study were explained to them.

Equipment

Five six-component sensors (Nano-17, ATI Industrial Automation, Garner, NC) were attached to a circular aluminum handle to which an aluminum beam (3.8 × 52.0 × 0.6 cm) was fixed (Fig. 1a). The recorded angular positions of the digits from the wooden circular object prehension were used to specify the angular positions of five force sensors. The sensors were aligned in the X–Y plane (a vertical plane). Aluminum caps were attached to the surface of each sensor. The bottom of the cap was flat and mounted on the surface of a sensor while the top part was round (the curvature k = 0.22 cm^{-1}) to accommodate the curvature of the circle shown as a dotted circle in Fig. 1a. Sandpaper [100-grit; static friction coefficients between the digit tip and the contact surface was 1.5; measured previously (Zatsiorsky et al. 2002)] was placed on the round contact surface of each cap to increase the friction between the digits and the caps. The radius (r_o^j) between the centre of the circular handle (O_G) and the contact surface was 4.5 cm for each sensor. The force components along the three orthogonal axes and three moment components about the three axes in the local reference system (LRS) for each sensor were recorded (Fig. 1b). A load (0.41 kg) was attached to the beam with an eyehook that could be positioned at seven different positions of the long beam with 10 cm intervals between adjacent positions. Positioning the weight at different positions produced different external torques on the handle system about the Z-axis (see the caption for Fig. 1). A plastic bubble level (Hi Vis Line Level, Stanley Tools, New Britain, CT) was positioned at the center of the horizontal beam so that subjects could monitor the consistent angular position of the handle and beam (Shim et al. 2003b). The total weight of the system, which consisted of the circular handle, beam, transducer, and suspended load, was 14.9 N.

A total of 30 analogue signals from the sensors were routed to two synchronized 12-bit analogue-digital converters (PCI-6031 and PCI-6033, National Instrument, Austin, TX) and processed and saved in a customized LabVIEW program (LabVIEW 7.1, National Instrument, Austin, TX) on a desktop computer (Dell Dimension E510, Austin, TX). The sampling frequency was set at 50 Hz.

Experimental procedure

The subjects washed their hands with soap and warm water to normalize the skin condition. The subjects were asked to hold a wooden circular handle (radius = 4.5 cm; the same size as the experimental handle used for force and moment recording) and the relative finger positions with respect to the thumb position were measured (index: 109.0° ± 12.6°, middle: 156.3° ± 11.2°, ring: 187.0° ± 8.2°, and little: 240.8° ± 15.4°; mean ± SD across subjects are presented). The subjects had a pre-testing session (two trials for each external torque condition) to be familiarized with the experimental procedure and testing-device. During the trials, the subjects sat in a chair and positioned their right upper arm on a wrist-forearm brace that was fixed to a table. The forearm was held stationary with Velcro straps. The upper arm was flexed 20° in the sagittal plane and the forearm was aligned parallel to the sagittal axis of the subject. For each trial, the subjects placed each digit on each six-component sensor and held the circular handle with the thumb at the top (Fig. 1a). The task for the subjects was to hold the handle with minimum effort while keeping the horizontal beam parallel to the transverse plane and maintaining the handle system in equilibrium. The task was achieved by monitoring and maintaining a bubble

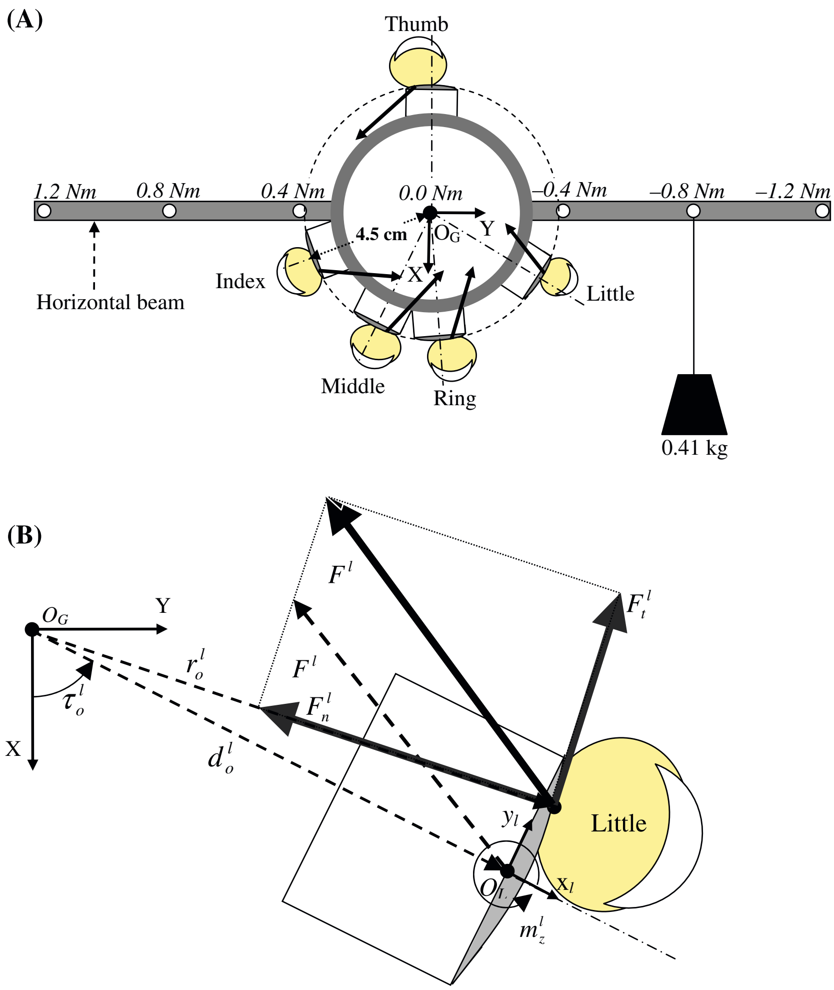


Fig. 1 **a** Schematic illustration of an aluminum handle (*gray circle with a large hollow inside*) and six-component sensors (*white rectangles*) at digit contacts. **b** Detailed schematic illustration of the little finger producing a force at a contact. O_G: origin of the global reference system of coordinates (GRS), X: X-axis in GRS, Y: Y-axis in GRS (Z-axis is not shown, but its direction follows the right-handed coordinate system and its positive direction is from paper to the reader), O_L: origin of local reference system of coordinates (LRS) of the little finger sensor, x_l: x-axis in LRS of little finger sensor, y_l: y-axis in LRS of the little finger sensor, m_z^l: moment about z-axis in LRS of little finger sensor (z-axis in LRS for each sensor is parallel to Z-axes in GRS), F^l: little finger force, F_n^l: little finger normal force, F_t^l: little finger tangential force, d_o^l: position of LRS origin in GRS, r_o^l: position of little finger centre of pressure (CoP) in GRS, θ_o^l: angular position of d_o^l in GRS. The LRS origin (O_L) was fixed to the center of the contact surface of the sensor and a cap (*shown gray*) was fixed on the sensor surface. The distance between the apex of the cap and O_L was ~0.81 mm. External torques were systematically changed by hanging the load at different positions along the horizontal beam. **b** Shows –0.8 Nm external torque condition. The figures are not drawn to scale

at the center of the bubble level (Shim et al. 2003b). The 0.41 kg load was located at seven different positions along the horizontal beam to create seven different external toques about Z-axis (i.e.,–1.2, –0.8, –0.4, 0, 0.4, 0.8, 1.2 Nm). The positive and negative torques required subjects to generate pronation and supination efforts, respectively. The pronation and supination efforts are respectively compatible to opening and closing efforts for a door knob and a jar cap in everyday circular object manipulations. To help the subjects achieve a stable trial-to-trial performance, the forearm, wrist, and hand positions were fixed and checked before every trial. In addition, the subjects were instructed to hold the circular handle exerting minimal force while placing the fingertip centers at the center of the sensor caps. Hyperextended joint configurations were not allowed for any phalangeal joints of the hand. Each subject performed 25 trials for each external torque condition. There were a total of 175 trials for each subject. Data recording started when a subject announced comfortable holding of the handle.

Before each trial, all signals from 30 channels were zeroed. The sampling frequency was 50 Hz and each trial was recorded for 6 s. A rest interval was given to the subject between trials and torque conditions to minimize fatigue. The minimum rest interval between trials and between torque conditions were 10 s and 5 min, respectively. The order of the external torque conditions was randomized and balanced.

Data analysis

The recorded force and moment data were averaged over the second half of the 6-s period for each trial for the following analysis. We analyzed normal and tangential forces in the X–Y plane and moments of tangential forces orthogonal to the plane. Since sticking a digit tip to the contact surface was not possible in this experiment [so-called 'soft contact model' (Mason and Salisbury 1985; Shimoga and Goldenberg 1996; Arimoto et al. 2001; Nguyen and Arimoto 2002)], a free moment (Zatsiorsky 2002; Shim et al. 2004b, 2005a) about the direction of a normal force was possible only due to the friction between the digit tip and the contact surface. However, we did not consider this component because it did not contribute to the task moment about the Z-axis and the magnitude of this component recorded was ignorable. The moment produced by each digit about the z-axis could be expressed as the sum of the moment produced by the force along the y-axis in LRS (F_y^j; directly recorded from the sensor) and moment about the z-axis at the center of the sensor surface (m_z^j) (Eq. 1). In the present experiment, the digits were not in direct contact with the sensors, but rather in contact with the sensor caps. The moment m_z^j is due to the distance from the LRS origin (O_L) where m_z^j was measured to the point on the sensor cap where the digit force was applied.

The force components measured in the LRS origin (O_L) were converted into the components in GRS using the direction cosines (Eq. 2). These components and the moment values about the Z-axis in GRS (M_Z^j) computed from Eq. (1) were then used to compute the tangential force components (F_t^j) at the digit contact on the cap (Eq. 3). The normal force component was calculated from Eq. (3). Note that the force measured at the LRS origin is equivalent to the force produced by the digit in terms of its magnitude and direction.

$$M_Z^j = m_z^j + d_o^j \times F_y^j, \quad j = \{thumb, index, middle, ring, little\} \tag{1}$$

$$\begin{bmatrix} F_X^j \\ F_Y^j \end{bmatrix} = \begin{bmatrix} \cos\theta_o^j & -\sin\theta_o^j \\ \sin\theta_o^j & \cos\theta_o^j \end{bmatrix} \begin{bmatrix} F_x^j \\ F_y^j \end{bmatrix}, \quad j = \{\text{thumb}, \text{index}, \text{middle}, \text{ring}, \text{little}\} \tag{2}$$

$$F_t^j = M_Z^j / r_o^j \text{ and } F_n^j = \sqrt{(F_X^j)^2 + (F_Y^j)^2 - (F_t^j)^2}, \quad j = \{\text{thumb}, \text{index}, \text{middle}, \text{ring}, \text{little}\} \tag{3}$$

VF normal and tangential forces (F_n^{vf} and F_t^{vf}) were calculated, respectively, as the sum of IF (index, middle, ring, and little) normal forces and the sum of IF tangential forces (Eq. 4). Note that the VF normal and tangential forces calculated in Eq. (4) are scalars. The IF normal forces or VF normal force do not produce a moment of force about the axis of rotation (O_G) because all IF normal forces pass through the axis of rotation and have zero moment arms (Eq. 5). VF normal and tangential forces are the sums of normal forces (i.e., grasping forces) and tangential forces (i.e., forces causing moments of force about O_G) of IF in each LRS, respectively. Hence, VF normal and tangential forces are not horizontal (Y-axis) and vertical (X-axis) forces in GRS because each axis in LRS is not parallel to the corresponding axis in GRS except Z-axis.

$$\begin{bmatrix} F_n^{\mathrm{vf}} \\ F_t^{\mathrm{vf}} \end{bmatrix} = \begin{bmatrix} \sum_{j=1}^{4} F_n^j \\ \sum_{j=1}^{4} F_t^j \end{bmatrix}, \quad j = \{\text{index, middle, ring, little}\} \tag{4}$$

$$M_Z = M_Z^{\mathrm{th}} + M_Z^{\mathrm{vf}} = r_o \times F_T^{\mathrm{th}} + r_o \times F_t^{\mathrm{vf}} = -T, \quad T \text{ represents an external torque} \tag{5}$$

For the 25 trials for each external torque condition, the variances of IF moments (Var_j, j = index, middle, ring, little) and the variance of the VF moment ($\mathrm{Var_{tot}}$) were computed across 25 trials for each external torque condition and each subject. The sum of the variances of IF moments ($\sum_{j=1}^{4} \mathrm{Var_j}$) was also computed across the trials. For further analysis, the difference between $\sum_{j=1}^{4} \mathrm{Var_j}$ and $\mathrm{Var_{tot}}$ was computed (Eq. 6) and normalized by $\sum_{j=1}^{4} \mathrm{Var_j}$ (Eq. 7).

$$\Delta\mathrm{Var} = \sum_{j=1}^{4} \mathrm{Var_j} - \mathrm{Var_{tot}}, \quad j = \{\text{index, middle, ring, little}\} \tag{6}$$

$$\Delta\mathrm{Var_{norm}} = \left[\sum_{j=1}^{4} \mathrm{Var_j} - \mathrm{Var_{tot}}\right] \Big/ \sum_{j=1}^{4} \mathrm{Var_j}, \quad j = \{\text{index, middle, ring, little}\} \tag{7}$$

Note, when $\Delta\text{Var} > 0$ and $\Delta\text{Var}_{\text{norm}} > 0$, negative covariations among the individual finger moments dominate, whereas when $\Delta\text{Var} < 0$ and $\Delta\text{Var}_{\text{norm}} < 0$, positive covariations among the individual finger moments prevail. These indices have been used as multi-digit synergy strength in previous studies to investigate covariation profiles between individual finger normal forces (Li et al. 1998; Shim et al. 2003a, 2004c, 2005b, 2006c; Shinohara et al. 2003, 2004). In this study, however, the indices are used to study synergic actions between individual finger tangential forces.

Statistical analysis

Mixed-effect ANOVAs with the factors of EXTERNAL TORQUE (seven levels: –1.2, –0.8, –0.4, 0, 0.4, 0.8, and 1.2 Nm), THUMB-VF (two levels: thumb and VF), and FINGER (four levels: index, middle, ring, and little fingers) were used to investigate the differences of dependent variables between experimental conditions and fingers at different hierarchical levels.

Linear regression was used to characterize the relations of variables. Pearson coefficients of correlation (r) were computed and then corrected for noise and error propagations (Taylor 1997) in MatLAB. The uncertainty or error affects the values of coefficients of correlation, i.e., the magnitudes of coefficients decrease with error propagations. The true coefficients of correlation, after the errors were eliminated, were computed [see Shim et al. (2003b) for computational details]. The true coefficients of correlation are usually larger in magnitude than the coefficients initially computed. In order to test the differences between two regression lines for negative and positive torque conditions, the slopes of the regression lines were statistically compared (Neter and Wasserman 1974).

For each external torque condition, sets of variables at the VF level (thumb and VF normal and tangential forces) were grouped, and coefficients of correlation between the variables were computed and corrected for noise and error propagations. The corrected correlations were used to construct a correlation matrix. This matrix was used to perform a principal component analysis (PCA) with a variance maximizing (varimax) rotation in MatLAB. The eigenvectors with eigenvalues >1 (Kaiser Criterion) were extracted as principal components (PCs) (Kaiser 1960) and the loading coefficients for each variable were calculated in the PCs. A customary cutoff loading coefficient of 0.4 was used as a minimal significant loading coefficient (Krishnamoorthy et al. 2003; Shim et al. 2005a).

Results

The virtual finger (VF) level

At the VF level of analysis, only the thumb and VF normal and tangential forces were considered, but the moments of normal and tangential forces were not included: moments of thumb and VF normal forces are always zero because the normal forces pass through the center of rotation (O_G in Fig. 1a) and the moment arms are all zero. The moments of thumb and VF tangential forces were not included because of the perfect linear relationship between the moments and the forces [i.e., the moments of tangential forces are simply calculated by multiplying the constant moment arm ($r_o =$ 4.5 cm) and the tangential forces].

VF and thumb force changes with external torque

The normal force magnitudes of both VF and thumb increased systematically with the external torque magnitude (Fig. 2a). For each external torque condition, the VF normal forces were always larger than the thumb normal forces. This finding is expected from the circular geometry of the handle which causes the non-parallel normal forces of individual fingers.

These findings were supported by two-way repeated-measures ANOVA with the factors of EXTERNAL TORQUE and THUMB-VF, which showed the significant effects of EXTERNAL TORQUE [$F(6,42) = 187.7$, $P < 0.001$], THUMB-VF [$F(1,7) = 1133.5$, $P < 0.001$], and EXTERNAL TORQUE × THUMB-VF [$F(6,42) = 19.7$, $P < 0.001$]. The tangential forces of the VF and thumb also increased with the external torque. The VF tangential force was larger than the thumb tangential force for the negative external torque conditions (supination effort by subjects) whereas the VF and thumb tangential forces for positive torque conditions (pronation effort by subjects) showed similar values. These findings were supported by two-way repeated-measures ANOVA with the factors of EXTERNAL TORQUE and THUMB-VF, which showed the significant effects of EXTERNAL TORQUE [$F(6,42) = 7321.6$, $P < 0.001$], VF force [$F(1,7) = 30.2$, $P = 0.001$], and EXTERNAL TORQUE × THUMB-VF [$F(6,42) = 64.3$, $P < 0.001$]. Thumb and VF normal forces increased linearly together for each torque direction (Fig. 2c). It was also true for the thumb and VF tangential forces (Fig. 2d). The ratios of the VF normal force to the thumb normal force were larger for positive torque conditions than for negative torque conditions (Fig. 2c) while the tangential forces were

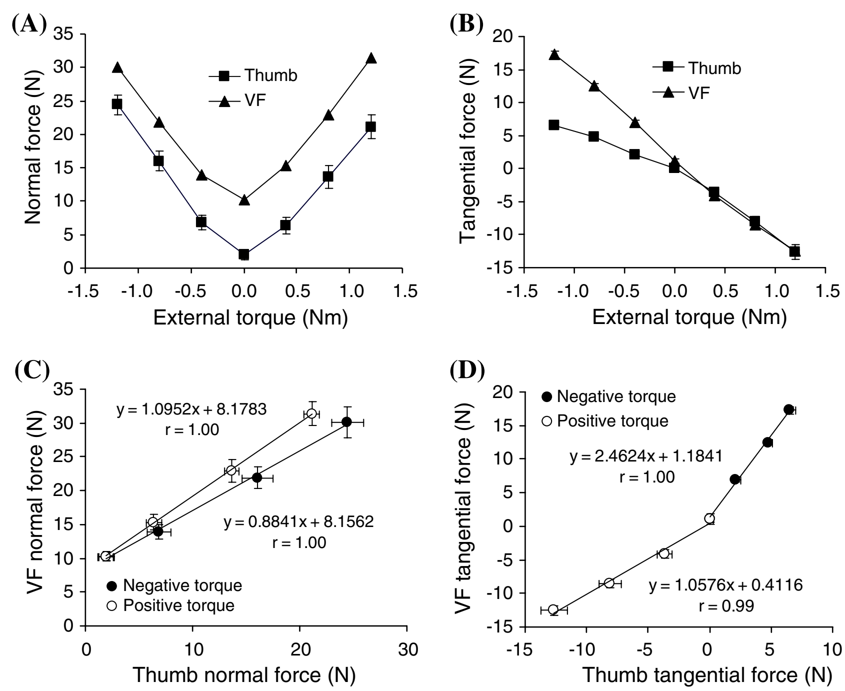


Fig. 2 Relations among forces under different external torque conditions at the virtual finger (VF) level. **a** Thumb and VF normal forces (F_n^{th} and F_n^{vf}). **b** Thumb and VF tangential forces (F_T^{th} and F_t^{vf}). **c** The VF normal forces versus thumb normal forces. **d** VF tangential forces versus thumb tangential forces. The positive and negative directional conventions are used for tangential forces to specify the directions of the moments produced by the tangential forces (e.g., a positive tangential force produce a positive moment). Averaged across subjects data are shown with standard error bars (some of the error bars are too small to be seen)

larger for negative torque conditions (Fig. 2d). These findings were supported by the significant ($P < 0.01$) differences of the slopes (1.0952 vs. 0.8841 in Fig. 2c and 2.4624 vs. 1.0576 in Fig. 2d) between the positive and negative torque conditions.

Inter-relations among VF and thumb normal and tangential forces

The trial-to-trial relations between the VF and thumb forces are shown in Fig. 3. The VF and thumb tangential forces are mechanically coupled in static equilibrium (Fig. 3b) because an increase in VF tangential force should accompany a decrease in thumb tangential force with the same magnitude and vice versa due to their relationship in static mechanics to keep the resultant moment equal and opposite to the external torque (Eq. 5). Thus, the high coefficients of correlation found between the VF and thumb tangential forces are expected (Fig. 3b). The large coefficients of correlation between the VF and thumb normal forces (Fig. 3a), on the other hand, are not necessitated by mechanics because the VF normal force is not required to be coupled with the thumb normal force (Eq. 4). However, the VF and thumb normal forces showed close-to-perfect coefficients of correlation for each external moment condition for each subject. In general, the magnitudes of coefficients ($|r|$) between the normal forces were even larger than those between the tangential forces.

Principal component analysis (PCA) on thumb and VF normal and tangential forces

The PCA on all VF level variables (thumb and VF normal and tangential forces; F_n^{th}, F_t^{th}, F_n^{vf}, and F_t^{vf}) revealed two PCs (PC1 and PC2) that accounted for 96.56 ± 0.95% (average ± SD across external torque conditions after the results were averaged across the subjects for each external torque condition) of the total variance. The loadings for each variable were calculated for PC1 and PC2 (Table 1). The thumb and VF *normal* forces had large loadings (absolute values > 0.64) in the same PCs (e.g., PC1 for –1.2, –0.8, 0, 0.4, 0.8, and 1.2 Nm and PC2 for –0.4 Nm in Table 1) and small (absolute values <0.35) loadings in the other PCs, whereas the thumb and VF tangential forces had large loadings in the latter PCs and small loading sin the former PCs. This data structure implies a decoupling between the normal forces of thumb and VF and the tangential forces of thumb and VF, which supports the principle of superposition. These findings were true for all external torque conditions in each subject. The large loadings of thumb and VF tangential forces in the same PCs and the opposite signs are necessitated by the static equilibrium: the mechanically necessitated negative correlation between the thumb and VF tangential

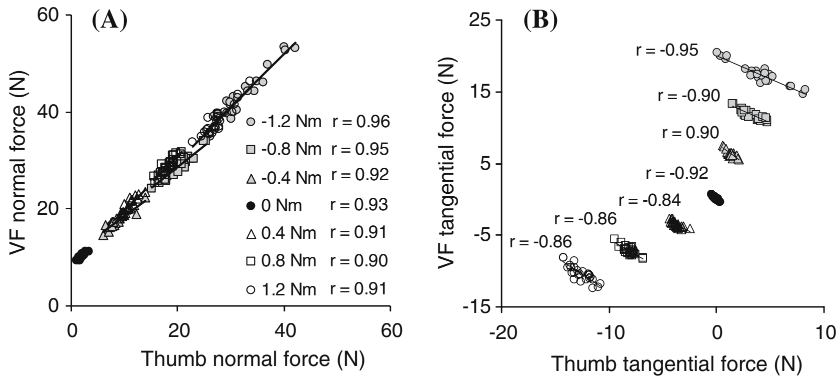


Fig. 3 Relations between (**a**) the thumb and VF normal forces (F_n^{th} and F_n^{vf}) and (**b**) the thumb and VF tangential forces (F_T^{th} and F_t^{vf}). All coefficients of correlation are significant ($P < 0.01$) and large in magnitudes ($|r| > 0.84$). The positive and negative directional conventions are used for tangential forces to specify the directions of the moments produced by the tangential forces (e.g., a positive tangential force produces a positive moment). The data are from a representative subject

Table 1 Loadings of principal components (PC1 and PC2) of all variables at the virtual finger (VF) level

	Variable	PC1	PC2
–1.2 Nm	F_n^{th}	**0.96**	–0.25
	F_T^{th}	–0.28	**0.94**
	F_n^{vf}	**0.97**	–0.22
	F_t^{vf}	0.20	**–0.97**
–1.8 Nm	F_n^{th}	**0.91**	0.35
	F_T^{th}	–0.34	**–0.84**
	F_n^{vf}	**0.96**	0.24
	F_t^{vf}	0.22	**0.97**
–0.4 Nm	F_n^{th}	–0.29	**0.93**
	F_T^{th}	**0.89**	–0.31
	F_n^{vf}	–0.24	**0.96**
	F_t^{vf}	**–0.96**	0.23
0 Nm	F_n^{th}	**0.98**	0.04
	F_T^{th}	–0.07	**0.98**
	F_n^{vf}	**0.98**	–0.03
	F_t^{vf}	–0.08	**–0.98**
0.4 Nm	F_n^{th}	**0.97**	0.10
	F_T^{th}	–0.24	**–0.85**
	F_n^{vf}	**0.91**	0.28
	F_t^{vf}	0.21	**0.89**
0.8 Nm	F_n^{th}	**0.93**	–0.22
	F_T^{th}	–0.27	**0.89**
	F_n^{vf}	**0.88**	–0.26
	F_t^{vf}	0.32	**–0.64**
1.2 Nm	F_n^{th}	**0.98**	0.03
	F_T^{th}	–0.11	**–0.94**
	F_n^{vf}	**0.97**	0.13
	F_t^{vf}	0.04	**0.97**

Note that F_n^{th} and F_n^{vf} have large loadings in PC1 or PC2 in which F_T^{th} and F_t^{vf} have relatively small loadings and vice versa. Data are from a representative subject

$F^{th}{}_n$ thumb normal force, F_T^{th} thumb tangential force, F_n^{vf} VF normal force (sum of finger normal forces), and F_t^{vf} VF tangential force (sum of finger tangential forces)

forces (Eq. 5). However, note that the large loadings of VF and thumb normal forces in the same PC are not completely required by the static equilibrium.

Variability of thumb and VF forces

The trial-to-trial variability of the thumb and VF normal and tangential forces increased with the external torque magnitude. The larger trial-to-trial variabilities for larger magnitudes of external torques are reflected in greater distributions of trial data points along the regression lines for larger magnitudes of external torques in Fig. 3a and b. The larger variability was found for the negative external torque conditions than the positive ones. These findings were supported by two-way repeated-measures ANOVAs with the factors of EXTERNAL TORQUE and THUMB-VF, which showed the significant effects of EXTERNAL TORQUE [$F(6,42) = 9.4$, $P < 0.001$] and THUMB-VF [$F(1,7) = 19.7$, $P < 0.005$] in normal forces and the significant effect of EXTERNAL TORQUE [$F(6,42) = 25.6$, $P < 0.001$] for tangential forces. The other factors or interaction effects were not significant. When the variability was plotted against the force magnitudes (Fig. 4c, d), the increasing trends of the variability with force magnitude were found.

In summary, the results from the analysis of thumb and VF showed that the normal and tangential force magnitudes of both VF and thumb increased systematically with the external torque magnitude. PCA showed a decoupling between the normal forces of thumb and VF and the tangential forces of thumb and VF, which supports the principle of superposition. In addition, the larger variability was found for the negative external torque conditions than the positive ones.

The individual finger (IF) level

At the IF level of analysis, the individual finger (index, middle, ring, and little) normal (F_n^j and F_n^j, j = index, middle, ring, little) and tangential forces (F_t^j and F_t^j) were considered.

IF force changes with external torque

The IF normal and tangential force magnitudes increased with the external torque magnitude (Fig. 5a, b). This finding was supported by two-way repeated-measures ANOVAs with the factors of EXTERNAL TORQUE and THUMB-VF, which showed the significant effects of EXTERNAL TORQUE [$F(6,42)$ = 122.6, $P < 0.001$], THUMB-VF [$F(3,21)$ = 60.6, $P < 0.001$], and EXTERNAL TORQUE × THUMB-VF [$F(18,126)$ = 46.2, $P < 0.001$] for normal forces and significant effects of EXTERNAL TORQUE [$F(6,42)$ = 95.7, $P < 0.001$], FINGER [$F(3,21)$ = 1390.3, $P < 0.001$], and EXTERNAL TORQUE × THUMB-VF [$F(18,126)$ = 30.0, $P < 0.001$] for tangential forces.

Variability of IF forces

The trial-to-trial variability of IF normal and tangential forces increased with the external torque magnitude (Fig. 6a, b). This finding was supported by two-way repeated-measures ANOVAs with the factors of EXTERNAL TORQUE and FINGER, which showed the significant effects of EXTERNAL TORQUE [$F(6,42)$ = 15.3, $P < 0.001$], FINGER [$F(3,21)$ = 19.3, $P < 0.001$], and EXTERNAL TORQUE × FINGER [$F(18,126)$ = 3.2, $P < 0.001$] for normal forces and the significant effects of EXTERNAL TORQUE [$F(6,42)$ = 54.7, $P < 0.001$], FINGER [$F(3,21)$ = 37.6, $P < 0.001$], and EXTERNAL TORQUE × FINGER [$F(18,126)$ = 12.1, $P < 0.001$] for tangential forces. When the variabilities were plotted against the force magnitudes (Fig. 6c, d), the normal and tangential forces showed 'rotated V-shape' and 'V-shape', respectively.

Finger synergy strength indices (ΔVar and ΔVar_{norm})

To quantify finger interactions during the moment production tasks, the indices (ΔVar and $\Delta \text{Var}_{\text{norm}}$) reflecting the difference between the sum of the variances of the moments of IF tangential forces and the variance of the resultant moment were computed (Eqs. 6, 7). Note that ΔVar and $\Delta \text{Var}_{\text{norm}}$ are multi-digit synergy indices. ΔVar and $\Delta \text{Var}_{\text{norm}}$ revealed positive values for all external torque conditions. This suggests that the negative covariations (i.e., error compensations) between IF moments prevail. ΔVar systematically increased with the external torque magnitude (Fig. 7a). ΔVar values were in general larger for negative external torque conditions than positive torque conditions. This finding was also true for

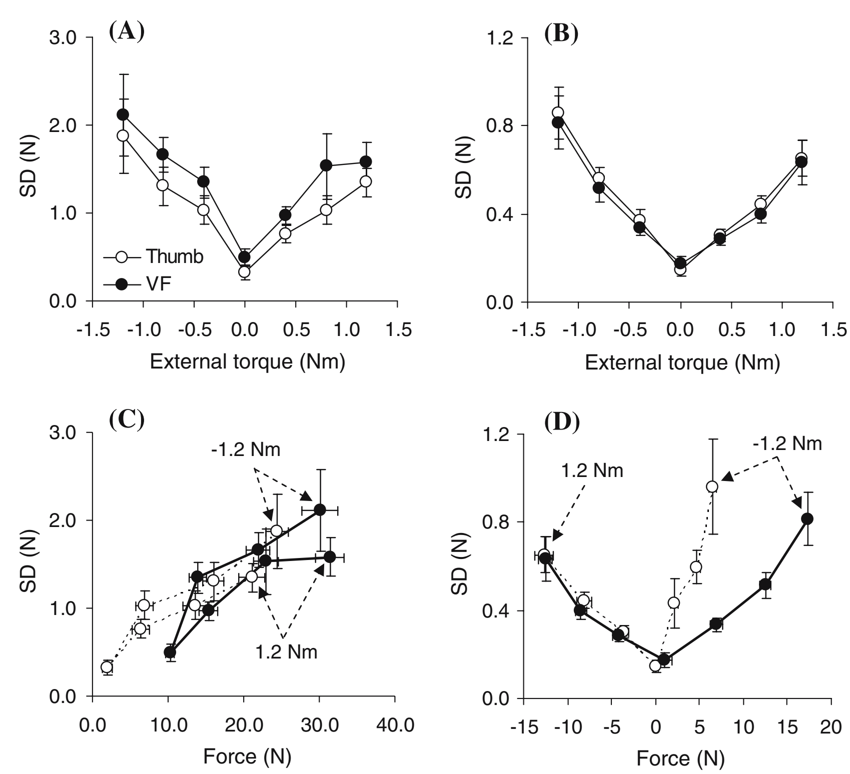


Fig. 4 Trial-to-trial variability of the thumb and VF (**a**) normal (F_n^{th} and F_n^{vf}) and (**b**) tangential forces (F_T^{th} and F_t^{vf}) under different external torque conditions. Trial-to-trial variability of the thumb and VF normal forces versus thumb and VF (**c**) normal forces and (**d**) tangential forces. The positive and negative directional conventions are used for tangential forces to specify the directions of the moments produced by the tangential forces (e.g., a positive tangential force produce a positive moment). Averaged across subjects data are shown with standard error bars

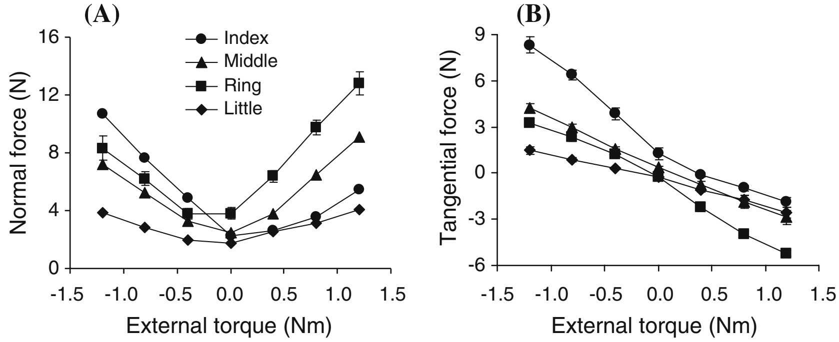
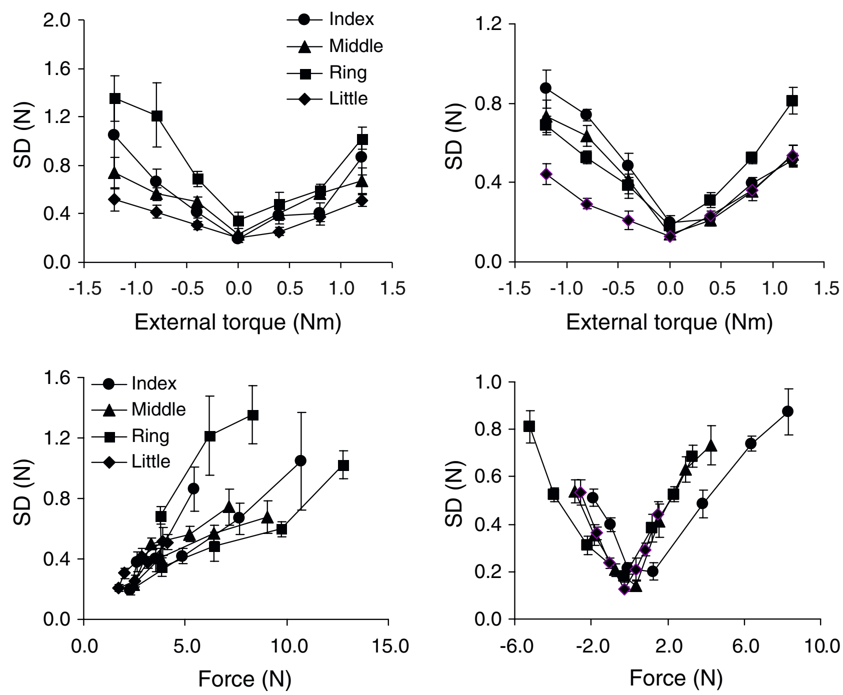


Fig. 5 Individual finger (**a**) normal forces (F^j_n, j = index, middle, ring, little) and tangential forces (F^j_t) under different external torque conditions. The positive and negative directional conventions are used for tangential forces to specify the directions of the moments produced by the tangential forces (e.g., a positive tangential force produces a positive moment). Averaged data across subjects are presented with standard error bars (some of the error bars are too small to be seen)

Fig. 6 Trial-to-trial variability of individual finger (**a**) normal (F^j_n) and (**b**) tangential (F^j_t) forces under different external torque conditions. Trial-to-trial variability of individual finger normal forces versus individual figner (**c**) normal forces and (**d**) tangential forces averaged across all trials. The positive and negative directional conventions are used for tangential forces to specify the directions of the moments produced by the tangential forces (e.g., a positive tangential force produces a positive moment). Averaged across subjects data are shown with standard error bars



ΔVar_{norm} (Fig. 7a) although the changes of ΔVar_{norm} (M-shape) with the external torque were different from those of ΔVar (V-shape). These findings were supported by one-way repeated-measures ANOVAs performed on ΔVar and ΔVar_{norm} with the factors of EXTERNAL TORQUE, which showed significant effects for ΔVar [$F(6,42) = 20.4$, $P < 0.001$] and ΔVar_{norm} [$F(6,42) = 3.4$, $P < 0.005$].

In summary, the magnitude and variability of individual finger normal and tangential forces increased with the external torque. The multi-digit synergy strength increased with the external torque magnitude. Generally, synergy strength was greater for negative external torque conditions than positive torque conditions.

Discussion

In this study, we investigated the trial-to-trial variabilities of digit forces and moments for the same multi-digit prehension tasks in order to test the hypotheses of the principle of superposition and the hierarchical organization of prehension control for circular object prehension. The PCA showed that the elemental variables were clearly decoupled into two groups: one group comprising normal forces and the other group containing tangential forces, which supports the first hypothesis. The synergy indices, ΔVar and ΔVar_{norm}, were always positive (negative covariations between IF moments), which confirms the second

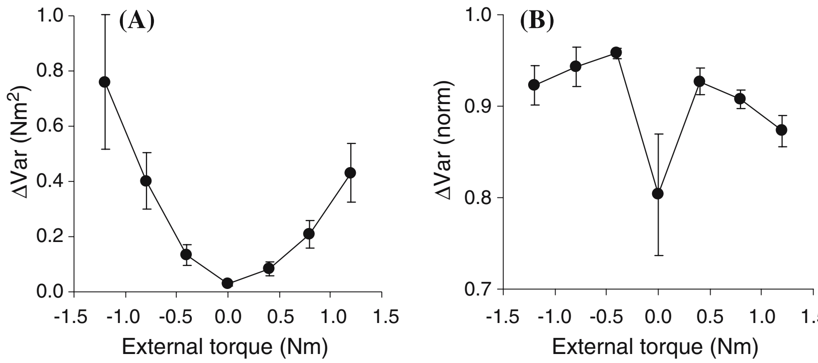


Fig. 7 **a** ΔVar and **b** normalized ΔVar (ΔVar_{norm}) computed over 25 trials for static prehension under different external torque conditions. Averaged data across subjects are presented with standard error bars

hypothesis. The discussion addresses the following topics: the principle of superposition in circular object prehension, hierarchical organization of prehension and the uncontrolled manifold (UCM) hypothesis, and trial-to-trial variability of forces.

Principle of superposition

The principle of superposition was originally suggested in robotics (Arimoto and Nguyen 2001; Arimoto et al. 2001, 2003) and has been confirmed in two-dimensional and three-dimensional prehension tasks in humans (Shim et al. 2003b, 2005a, 2006c).

During static prehension of an upright rectangular object, there exist two static constraints to be satisfied: all forces should cancel out to be zero ($\sum \overrightarrow{F^j} = 0$) and all moments should cancel out to be zero ($\sum \overrightarrow{M^j} = 0$) in all three-dimensions. At the level of virtual finger (Cutkosky and Howe 1990; Iberall 1997; Yoshikawa 1999; Baud-Bovy and Soechting 2001; Santello et al. 2002), two groups of the variables are already necessitated by static mechanics during a rectangular object prehension: the thumb grasping force and the VF grasping force (sum of individual finger normal forces) should have the same force magnitudes along the horizontal axis (i.e., $F_n^{vf} = F_n^{th}$; vf and th respectively stand for virtual finger and thumb, and n represents a normal force) while the sum of the thumb tangential force (load force) and the VF tangential force should be equal and opposite to the weight of the hand-held object along the vertical axis (i.e., $F_t^{vf} + F_t^{th} = -W$; t represents a tangential force and W stands for the weight of a hand-held object). The other group of variables, the tangential forces and moments of normal and tangential force, are also coupled. The mechanically necessitated coupling relationship between these variables has been explained using the 'chain effects' (i.e., high correlations between seemingly unrelated variables can be explained by chained relations between variables (Gregory 2002; Zatsiorsky et al. 2003; Zatsiorsky and Latash 2004; Shim et al. 2005a). Therefore, the novel finding of the previous studies (Shim et al. 2003b, 2005a) on the principle of superposition in human prehension was the decoupling of the two groups of variables or two synergies, rather than the coupling of variables in each synergy. Therefore, there are two independent synergies used by the CNS to control two important aspects of the prehension of a rectangular object: grasping stability control by the thumb and VF normal forces and rotational equilibrium control by the thumb and VF tangential forces and the moments of forces. Shim et al. (2006b) recently showed that the stabilizations of grasping forces and grasping moments can be modulated in different directions after mechanical perturbations (sudden changes of weight of the hand-held object and/or sudden changes of external torques) are given. The study suggested that the CNS may be more concerned about rotational equilibrium control than grasping stability control when a mechanical perturbation is given to the hand-held object.

Our study on circular object prehension revealed relationships of elemental variables (thumb and VF normal and tangential forces) similar to the rectangular object prehension tasks of previous studies. The PCA revealed two PCs: thumb and VF normal (tangential) forces had large (small) loadings in one PC, but small (large) loadings in the other. This data structure suggests two null spaces or two independent multi-digit synergies. This finding may not be easily expected without experiments because the relationship between the thumb and VF normal forces are not mechanically necessitated in circular object prehension although it is in rectangular object prehension. It appears that the grasping stability and the rotational equilibrium are controlled by two independent central commands during circular object prehension as it was previously suggested in rectangular object prehension. Thus, this finding supports the principle of superposition for circular object prehension.

The findings from PCA and ΔVar and ΔVar_{norm} analysis also support the previously suggested central neural back-coupling model (CBC-model) for multi-digit actions (Latash et al. 2005b), because in the CBC-model the performance variables related to 'force stabilization' and 'moment stabilization' can be separately modulated as it was shown in the results from our experiments.

Hierarchical organization of prehension and uncontrolled manifold (UCM) hypothesis

The earlier finger movement experiments from skilled telegraphers (Bryan 1899) and typists (Book 1908) suggested the hierarchical organization of finger movements by demonstrating that lower level units (e.g., letters) were combined as upper level unit (e.g., word) for typing control. The following physiological and behavioral experiments in the mid twentieth centuries (Weiss 1941; Sherrington 1947; Turvey 1977) facilitated the conceptualization and theorization of hierarchical organization of human behavior [see (Gallistel 1980) for details].

In this study we have shown that there exist positive multi-digit synergy indices for all external torque conditions. This means that the IF moments had dominant negative covariations, resulting in stabilized performance of the VF moment (sum of IF moments). These results conspicuously support the hierarchical organization of prehension, i.e., the individual fingers are acting together to stabilize the functionally important performance of the VF. The stabilization of the overall performance of individual finger actions have been well described for rectangular object prehension (Shim et al. 2003b, 2004a, 2004c, 2005a, 2006c) and far more for multi-finger pressing (Shim et al. 2003a, 2005b; Latash et al. 2004b; Kim et al. 2006). All these studies used digit interaction indices to study how the CNS controls multiple digits during prehension and pressing. This approach is similar to previously suggested UCM hypothesis (Scholz and Schoner 1999; Latash et al. 2002; Kang et al. 2004). According to UCM hypothesis, the CNS specifies a subspace (UCM) in the state space of elemental variables for a redundant motor system and tries to find a solution for a task in the subspace while allowing solutions in the UCM, yet compressing the variability orthogonal to the UCM (UCM_{orth}). Thus, for a successful manipulation task, the sum of the trial-to-trial variabilities (e.g., $\sum_{j=1}^{4} Var_j$ or variability in UCM) of individual finger actions (e.g., forces/moments) may be relatively large, whereas the variability of the combined finger actions (e.g., Var_{tot} or variability in UCM_{orth}) can be small. The previous UCM analysis on multi-digit pressing removed inter-digit dependency [called finger force enslaving (a phenomenon of unintended force production by non-task fingers during a task finger force production) (Reilly and Hammond 2000; Zatsiorsky et al. 2000)] in order to extract independent elemental variables, called 'Modes' (Danion et al. 2003; Kang et al. 2004; Olafsdottir et al. 2005a). The Modes have been considered as hypothetical independent elemental variables or central commands to fingers, and the UCM analysis for finger force studies used Modes to investigate the synergic actions between the Modes.

The inter-dependent digit actions during pressing are contributed by peripheral and central intrinsic factors such as insertions of a flexor digitorum profundus to multiple fingers (von Schroeder et al. 1990; von Schroeder and Botte 2001; Kilbreath et al. 2002) and motor cortex (M1) outputs diverging to innervate the spinal motor neuron pools of different finger muscles (Shinoda et al. 1979; Fetz et al. 1980; Buys et al. 1986). However, during a free object prehension, the inter-dependent digit actions are caused by not only the intrinsic factors but also the external constraints imposed by the task mechanics. For example, when the thumb increases its normal force in static circular object prehension as in our experiment, other fingers will produce enslaving forces due to the intrinsic finger dependency to the thumb (Olafsdottir et al. 2005b). However, if the resultant force of the finger enslaving forces is not the same and opposite to the thumb force, the fingers will be required to adjust the forces to compensate the difference between the thumb force and the finger resultant force or VF force. In our study, we did not remove the inter-digit dependency for the investigation of synergic actions between fingers due to technical difficulties (e.g., differentiating the contributions of intrinsic factors from the contributions of the mechanical constraints during prehension of the free circular handle). However, if we assume that the direction of enslaving actions of non-task digits are the same as the direction of task digits as implied by the previous studies (Lang and Schieber 2004; Shim et al. 2006b), removing the inter-digit dependency would have caused changes in ΔVar and ΔVar_{norm} values to be more positive. This would suggest larger error compensations between fingers because the inter-digit dependency makes the finger actions positively covary.

Active control of tangential forces

The tangential force during grasping has been considered to be passively coupled (Flanagan and Wing

1995; Pheasant and O'Neill 1975) by other mechanical constraints such as grasping normal force (Rohles et al. 1983; Nagashima and Konz 1986; Imrhan and Loo 1988), handle diameter (Pheasant and O'Neill 1975; DJ and MW 1986; Nagashima and Konz 1986; Adams and Peterson 1988; Imrhan and Loo 1988), contact surface condition (Amis 1987; Lee and Rim 1991; Radhakrishnan and Nagaravindra 1993; Gurram et al. 1995; Kinoshita and Francis 1996; Hall 1997; Johansson 1998), orientation of a handheld object (Pataky et al. 2004), and inertial force (Zatsiorsky 2005).

It was previously shown that the finger normal forces during pressing and prehension can be synergically controlled by the CNS to stabilize the task-specific performances (reviewed in Latash et al. 2004a). Previous studies on synergic finger actions during pressing used the index synergy (i.e., ΔVar) to study the interactions between the finger pressing forces (normal forces) (Li et al. 1998; Shinohara et al. 2003).

Other studies on multi-digit prehension of a rectangular object used the index of synergy calculated from the normal forces of individual fingers or the moments of individual fingers (Shim et al. 2004c, 2005b, 2006c).

Contrary to the previous studies on rectangular object prehension, the geometry of a circular object employed in the current study does not allow finger normal forces to produce moments of force about the center of the circular object. Thus, the tangential forces are the only forces contributing to the moments which achieve the rotational equilibrium of the circular object against external torques. The index of synergy calculated from the tangential forces showed synergic actions between individual finger tangential forces for stabilizing the virtual finger tangential force. Thus, this result suggests that finger tangential forces can be actively controlled by the CNS.

Trial-to-trial variability of forces

Due to the obvious importance of accurate force production in everyday activities, the variability of force has been an interest of many researchers in human motor control (Fullerton and Carttell 1892; Michon 1967; Newell and Carlton 1988; Newell and Corcos 1993; Moritz et al. 2005; Sosnoff and Newell 2006). The experimental tasks employed in the current study were designed to encourage the subjects to produce a consistent prehension performance across multiple trials under the same external torque conditions. Despite the effort, the trial-to-trial variabilities of forces were significant at both VF and IF levels.

The thumb and VF tangential force variabilities showed very similar values for each external torque (Fig. 4b), whereas the thumb normal force variability was always larger than the VF normal force variability. The identical variability trend of the thumb and VF tangential forces can be simply explained by the moment constraint $(\sum \vec{M^j} = 0)$ of static prehension (Eq. 5). Since the resultant moment produced by the thumb and VF should be equal and opposite to the external torque, the moment of thumb tangential force and the moment of VF should show close-to-perfect negative correlations for an ideal performance: an increase in one should be followed by a decrease in the other with the same magnitude. The moments of thumb and VF tangential forces are calculated by multiplying the thumb and VF tangential forces by the constant radius (4.5 cm) of the circular handle. Thus, the thumb and VF tangential forces should also have close-to-perfect negative correlations. Due to this relationship, an increase in thumb tangential force should correspond to a decrease in VF tangential force with the same magnitude, resulting in the same variability (SD) as shown in Fig. 4b. The larger variability of the VF normal force than the thumb normal force can be explained from the non-parallel force directions between the thumb and IF normal forces. Since the IF normal forces are not parallel to the thumb normal force, an increase in the thumb normal force with a certain magnitude in the vertical direction should correspond to an increase in the sum of the IF normal forces with a larger magnitude to satisfy the force constraint $(\sum \vec{F^j} = 0)$ in the vertical direction. This relationship resulted in the larger VF normal force variability than the thumb normal force variability.

In general, larger force variabilities were found in negative external torque conditions (supination effort for subjects) for both thumb and VF normal and tangential forces (Fig. 4a, b). These findings reflect an ability of the CNS control to the hand and lower arm muscles to generate more consistent force outputs in pronation than supination during static circular object prehension. Previous studies showed that the strength of subject is inversely related to the control of end-effector force or torque (Shinohara et al. 2003; Hamilton et al. 2004; Sosnoff and Newell 2006). Hamilton et al. (2004) recorded the maximum voluntary torques from four different muscle groups in the arm. They showed that the coefficients of variation of torque decreased systematically as the maximum voluntary torque increases. Sosnoff and Newell (2006) asked subjects to consistent force output of 5 or 25% maximum voluntary force and found that the variability of force output decreased with the maximum voluntary force. A previous study on strength training effects on finger control showed that training finger muscles with heavy loads increased both consistent force outputs and functional hand dexterity (Bilodeau et al. 2000). If muscle strength is a major factor to determine the consistency of finger force outputs as suggested in the previous studies, the large thumb and index finger abductors producing pronation torques during circular object prehension (e.g., thenar muscles of the thumb and dorsal interossei for the index finger) may have played a role in the small variability in the constant torque production tasks during pronation as compared to supination. However, the result of the current study that showed smaller variability during pronation and our previous studies that showed smaller maximum voluntary torque in pronation as compared to supination (Shim et al. 2004a, 2006a) seem to be contradictory to the previous studies by others. Thus, it seems that the different between the pronation and supination torque control found in the current study seems to be contributed to by the specificity of different muscle groups involved in the pronation and supination tasks.

The synergy strength indices, ΔVar and ΔVar_{norm}, are similar to negated covariations between the IF moments: the positive and negative ΔVar and ΔVar_{norm} represent prevalent negative and positive covariations between variables, respectively. When the large variability was present for negative external torque conditions, the larger error compensations between IF moments, indexed by the larger ΔVar and ΔVar_{norm} values for the negative external torque conditions, were observed in our study. Thus, it appears that the CNS uses the strategy to generate larger error compensations between IF moments for the tasks in which larger variabilities are present.

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