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Prehension synergy: Effects of static constraints on multi-finger prehension

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ABSTRACT

Previous studies have shown that the interactions of human hand digits are influenced by internal constraints, i.e., biomechanical and central constraints. However, little is currently known about the influence of externally imposed mechanical constraints on multi-finger behavior. This study investigates maximal digit force production during fixed object and free object prehension in statics. The results from the fixed object prehension indicated that the closer the non-task finger was positioned to the task finger, the greater the force produced by the non-task finger, which supports the proximity hypothesis. Conversely, the non-task fingers with longer moment arms showed greater force production during free object prehension, which supports the mechanical advantage hypothesis. During the free object prehension, equal and opposite torques were produced by the digit normal forces and tangential forces, while this phenomenon was not observed in the fixed object prehension. The results also showed that the thumb normal force had a positive linear relationship with task-finger normal forces during fixed object prehension while the thumb normal force remained constant during free object prehension tasks. We concluded that the CNS employed different strategies when different sets of internal and external constraints are provided during multi-digit prehension tasks.

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1. Introduction

Previous studies on multi-finger actions have focused on two main topics, the synergistic actions of multiple fingers (Danion, Latash, Li, & Zatsiorsky, 2001; Kang, Shinohara, Zatsiorsky, & Latash, 2004; Krishnamoorthy, Latash, Scholz, & Zatsiorsky, 2003; Latash, Li, Danion, & Zatsiorsky, 2002; Santello & Soechting, 2000; Shim, Latash, & Zatsiorsky, 2005; Visser et al., 2003) and the independent actions of the individual fingers (Edin, Westling, & Johansson, 1992; Hager-Ross & Schieber, 2000; Kilbreath & Gandevia, 1994; Schieber, 1995). Many studies on finger independence have shown that the independent actions of fingers are influenced by internal constraints, such as biomechanical and central constraints. For example, biomechanical constraints affecting independent finger actions include the interconnection of tendons in the hand and forearm (Hager-Ross & Schieber, 2000; Leijnse, Walbeehm, Sonneveld, Hovius, & Kauer, 1997). The flexor digitorum profundus (FDP) has insertions in all four fingers. This multi-tendoned extrinsic muscle, when activated, induces the movements or force production of adjacent fingers when another intended finger moves or produces force (Kilbreath, Gorman, Raymond, & Gandevia, 2002; Li, Zatsiorsky, & Latash, 2000; Reilly & Schieber, 2003; Schieber, 1995; Thompson & Giurintano, 1989). One of the central constraints includes the short-term synchronization of motor units that cause simultaneous actions of multiple fingers. When more than two motor units receive a common neural input, multiple motor units are excited simultaneously (Reilly & Schieber, 2003; Schieber, 1996; Winges, Kornatz, & Santello, 2008). Although many previous studies showed that the independent actions of fingers are affected by these internal constraints created by the human body, it is still largely unknown how external constraints, the constraints provided by the physical world with which the human body interacts, affect finger actions during multi-digit grasping.

Previous studies on multi-finger force production tasks have commonly revealed that greater forces are created in non-task fingers the closer these fingers are to the task fingers, and have suggested that this phenomenon supports the proximity hypothesis (Olafsdottir, Zatsiorsky, & Latash, 2005; Zatsiorsky, Li, & Latash, 2000). Previous studies have also supported the mechanical advantage hypothesis in moment production tasks during the multi-digit grasping of a mechanically fixed object (Shim, Latash, & Zatsiorsky, 2004; Zatsiorsky, Gregory, & Latash, 2002). The normal forces of peripheral fingers (i.e., index and little fingers) are produced mainly in response to the external torques. Consequently, they especially depend on the external torques since they have longer moment arms resulting in greater mechanical advantages. The force productions by central fingers (i.e., middle and ringer fingers with shorter moment arms) depend on the external torques as well as the load magnitudes (Zatsiorsky et al., 2002). This implies that the fingers with longer moment arms are mainly torque generating fingers. According to the mechanical advantage hypothesis, the force effectors located farther away from the axis of rotation have greater mechanical advantages due to the longer moment arm. In other words, the specific functions of motor effectors would be determined by the requirements for the successful completion of the task, such as moment production or rotational equilibrium against external torques (Devlin & Wastell, 1986; Frey & Carlson, 1994; Smutz et al., 1998).

Despite these earlier studies, it is still unknown if the central nervous system (CNS) uses the mechanical advantage hypothesis by applying the force production in non-task fingers during free-object grasping tasks. The multi-finger grasping of a free object and the grasping of a mechanically fixed object are governed by different sets of constraints. In order to engage in the static grasping of a free object, the CNS needs to satisfy the resultant force and resultant moment of force constraints. For example, the sum of all digit forces and moments applied to a free object should be equal to zero, so that there is no movement of the object. However, the CNS does not need to consider these static external constraints when manipulating a mechanically fixed object.

The main purpose of the current study is to investigate the independent actions of individual digits and the interactions of multiple digits while holding a mechanically fixed object or a free object. We assume that the CNS only needs to satisfy internal constraints (i.e., biomechanical and central constraints) when holding a mechanically fixed object, while it is required to satisfy both internal and external constraints (i.e., translation and rotational equilibrium constraints) when holding a free object. This study was specifically designed to investigate the strategies used by the CNS under the rotational equilibrium constraint (see Section 2.2) and tests three hypotheses. The first hypothesis under investigation is the proximity hypothesis in mechanically fixed object prehension, which suggests that the CNS will produce greater forces from the non-task fingers closer to the task finger in maximum finger force production tasks during a mechanically fixed object prehension. The second hypothesis under investigation is the mechanical advantage hypothesis in free object prehension, which suggests that the CNS would produce greater forces from the non-task fingers with longer moment arms during free object prehension. Finally, it is hypothesized that the CNS utilizes the tangential force actively in maintaining rotational equilibrium during free object prehension, in contrast to the CNS's control strategy for the tangential force during a fixed object prehension.

2. Methods

2.1. Participants

Ten male volunteers (age: 25.2 ± 3.1 years, weight: 71.1 ± 1.2 kg, height: 175.2 ± 3.3 cm, hand length: 19.7 ± 1.4 cm, and hand width: 9.1 ± 0.8 cm; mean ± *SD* across participants are presented) participated in this experiment. All participants were right-handed as determined by the Edinburgh Handedness Inventory (Oldfield, 1971). The hand length was measured using the distal crease of the wrist to the middle fingertip when a given participant 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 using the radial side of the index finger metacarpophalangeal joint to the ulnar side of the little finger metacarpophalangeal joint. Before testing, the experimental procedures of the study were explained to the participants and they signed a consent form approved by the University of Maryland's Institutional Review Board (IRB).

2.2. Equipment

Five six-component (three force and three moment components) transducers (Nano-17s, ATI Industrial Automation, Garner, NC, USA) attached to an aluminum handle were used to measure each individual digit's forces and moments (Fig. 1a). In order to monitor the position of the handle and to provide feedback about the handle position to the participant during the free object prehension tasks, a six-component (three position and three angle components) magnetic tracking device (Polhemus LIBERTY, Rockwell Collins Co., Colchester, VT, USA) was used. A Polhemus position-angle sensor was attached to the front edge of a Plexiglas base (0.2 cm × 17.0 cm × 13.5 cm). This Plexiglas base was affixed to the top of the handle. Pieces of 100-grit sandpaper with a friction coefficient of about 1.5 were attached to the surface of each sensor in order to increase the friction between the digits and the force application point. The vertical distance between the adjacent sensors for index, middle, ring, and little fingers was 30 mm. The thumb sensor was positioned at the midpoint between middle and ring finger sensors. The horizontal distance between the contact points of the thumb sensor and other sensors was 70 mm. A counter-load (300 g) with the same weight as the handle (including the sensors) was used to eliminate the effect of gravity (Fig. 1b). Because of this counter-load, the sum of digits' tangential forces did not have to be equal to the weight of the handle when the handle was vertically oriented (Shim, Lay, Zatsiorsky, & Latash, 2004). This preparation was done to focus our investigation on the rotational constraint during participants' grasping of the handle in the air (i.e., free-object grasping). The analogue signals were routed to a 12-bit analogue-digital converter (a PCI-6031 and a PCI-6033, National Instrument, Austin, TX). LabView programs (LabView 7.1, National Instrument, Austin, TX) were developed and used to synchronously record the signals from the force/moment sensors and magnetic sensor. The sampling frequency was set at 50 Hz. The sampled data were digitally low-pass filtered with a 2nd order Butterworth filter. The cutoff low frequency was set at 5 Hz (Gao, Latash, & Zatsiorsky, 2005a; Li, Latash, & Zatsiorsky, 1998).

2.3. Experimental procedure

The participants sat in a chair facing the computer screen and positioned their right upper arm on a wrist-forearm brace (a semi-circular plastic cylinder) that was fixed to a table (Shim, Latash,

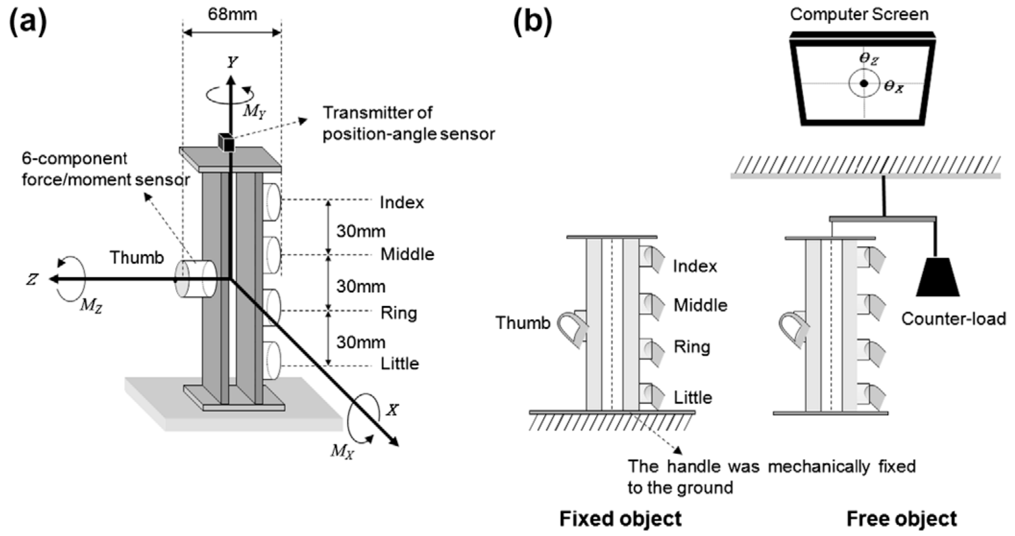

Fig. 1. (a) The customized handle: the force–moment sensors shown as white cylinders were attached to two vertical aluminum bars. The participants were instructed to place each digit on the designated sensor (i.e., Thumb, Index, Middle, Ring, and Little) and keep all digits on the sensors during trials. The transmitter of a magnetic position-angle sensor, marked out 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) For the fixed object, the handle was mechanically fixed to a desk and could not be moved by digits' forces (left). The participant held the handle while monitoring its angular position about *X*- and *Z*-axes during free object prehension (right). These positions were designated θ_X and θ_Z, respectively. A counter-load of 300 g, the same weight as the handle and sensors, was hung to the long horizontal wooden beam.

& Zatsiorsky, 2003). The forearm was held stationary with Velcro straps to prevent forearm and wrist movements. There were five single-digit maximal voluntary force (MVF) production tasks along the *Z*-axis (T, I, M, R, L) and one multi-digit MVF task along the same axis (TIMRL): These were designated as the T- (thumb); I- (index finger); M- (middle finger); R- (ring finger); and L- (little finger) tasks. The multi-digit task was designated the TIMRL-task. Note that the participants were instructed to keep all digits on the sensors during each task and were asked to pay attention to the task-digit maximal force production while allowing non-task digit force productions. It was not allowed to lift non-task fingers during the trials. All digit forces were recorded during all trials and tasks. Two different experimental conditions were used in order to investigate the effects of rotational equilibrium constraint on the finger force production during multi-finger grasping. One condition included MVF tasks while holding a fixed object and the other included the same tasks holding a free object. For the fixed object condition, the handle was mechanically fixed to a desk and could not be moved. During the free object condition, participants watched real-time feedback of the angular position of the handle about the *X*- and *Z*-axes. They were instructed to avoid handle rotations and were asked to minimize the angular deviation of the object. If the angular deviation exceeded the pre-defined criteria $\left(\sqrt{\theta_X^2 + \theta_Z^2} > 1^\circ\right)$ during the trial, the data collection automatically stopped and the participant performed the trial again (Shim et al., 2003). For each condition, the participant performed three consecutive attempts. Thus, each participant performed a total of 36 trials (2 tasks × 6 MVF tasks × 3 attempts = 36 trials). The LabView program automatically initialized the values of sensor signals to zero at the beginning of each trial. Two-minute breaks were given at the end of each trial in order to avoid fatigue effects. Prior to the actual experiments, the participants had a familiarization session, which included an explanation of the experimental procedures and several practice trials. The order of the six MVF tasks was balanced and no participant reported fatigue.

2.4. Data analysis

The maximal forces of the task digit and non-task digits at the instant maximal force production of the task digit were obtained. The participants performed three attempts for each condition, and the average data over three attempts were calculated for further analysis. The analysis was limited to the frontal plane of the participant (the *Y–Z* plane in Fig. 1a). Forces along *Y*- and *Z*-axes, tangential and normal forces, respectively, and the moments produced by these two forces (moments about *X*-axis) were considered. The force application point was calculated from $y = -M_x/F_z$ along the *Y*-axis, with respect to the center position of the each sensor, where M_x is the moment of force about the local *X*-axis and F_z is the force along the *Z*-axis (the normal force component). The total moment exerted by digit forces about the *X*-axis was calculated from Eq. (3). The participant performed three attempts in each condition. Their individual trial data were averaged and used for further analyses.

2.4.1. Model

During the fixed object prehension, the handle was mechanically fixed to the immovable table so that there was no rotational equilibrium to be satisfied. During the free object prehension, however, the following three mechanical constraints should be satisfied in order to maintain static equilibrium along *Z*-axis.

(1) The sum of the normal force of all four fingers should be equal to the normal force of the thumb

$$F^n_{th} = F^n_i + F^n_m + F^n_r + F^n_l = \sum_j F^n_j, j = \{i, m, r, l\} \tag{1}$$

(2) The sum of the digit tangential forces should be equal to zero. Note that the counter-load, which provided the exact same weight as the handle including the sensors, was used. Because of this, the resultant tangential force of all digits should be zero in order to maintain static equilibrium along the *Y*-axis

$$F^t_{th} + F^t_i + F^t_m + F^t_r + F^t_l = 0 \tag{2}$$

(3) The resultant moment created by the digit forces should be zero due to the task constraints (e.g., the rotational constraint),

$$M_{TOT} = -\underbrace{F^n_{th}d_{th} + F^n_i d_i + F^n_m d_m + F^n_r d_r + F^n_l d_l}_{\text{Moment of normal force } (M_n)} + \underbrace{F^t_{th}r_{th} + F^t_i r_i + F^t_m r_m + F^t_r r_r + F^t_l r_l = 0}_{\text{Moment of tangential force } (M_t)} \tag{3}$$

where the subscripts *th, i, m, r*, and *l* stand for the thumb, index, middle, ring and little finger, respectively. The superscripts *n* and *t* indicate the normal and tangential force components. *d* and *r* represent the moment arms of the normal and tangential forces, respectively, orthogonal to the each force component. Theoretically, *d* can be changed during the trials due to finger tip movement along the *Y*-axis, while *r* is a constant (equal to half of the grip width).

2.4.2. Finger inter-dependency index (FII)

The finger inter-dependency (i.e., finger enslaving) was defined as the average non-task-finger forces normalized by the task finger MVF ($F^j_{\max}$). In order to quantify the digit inter-dependency, the following calculation was used (Shim et al., 2008; Zatsiorsky et al., 2000):

$$FII_j = \left[\left(\sum_{i=1}^{n} F^{ij} \Big/ F^j_{\max}\right)/n - 1\right] \times 100\% \tag{4}$$

where $i \neq j, n = 4$. F^{ij} is a force production by non-task finger (i) during the j finger maximum force task. Normal force components of fingers were used for this calculation.

2.4.3. Proximity index (PXI)

In order to test the proximity hypothesis (the idea that the closer the non-task fingers are to the task finger, the greater the enslaving force produced), a proximity index (PXI_k) was calculated as the average value of non-task-finger forces across the anatomical rank from the task fingers (Zatsiorsky, Li, & Latash, 1998; Zatsiorsky et al., 2000). Non-task-finger forces were normalized by the individual finger maximal force measured during the single-finger MVF task (Eq. (5))

$$PXI_k = \left[\sum^{m} \left(F^k / F^k_{\max}\right) \Big/ m\right] \times 100\% \tag{5}$$

where k represents the first, second, and third adjacent fingers to the task finger. During middle finger task, for example, k = 1 for the index and ring fingers and k = 2 for the little finger. F^k is a force production by the kth non-task finger. $F^k_{\max}$ is the maximal force produced by the kth finger during single-finger MVF task. m indicates the number of non-task fingers within each calculation of the first-, second-, and third-ranked non-task fingers. PXI represents the non-task-finger force averaged across the finger of the same anatomical ranks. The normal force components of fingers were used for this calculation.

2.4.4. Mechanical advantage index (MAI)

In order to test the mechanical advantage hypothesis, non-task fingers were classified into two types of antagonist (ANT) fingers based on the different moment arms caused by parallel finger connections. The moment arm of antagonist 2 (ANT2) is longer than that of antagonist 1 (ANT1). ANT fingers produce the opposite directional moment to the moment of the task fingers. For example, when the task finger is an index finger, the direction of the moment of normal force by the middle finger is equal to that by index finger (i.e., agonist) while the normal forces of the ring and little finger would produce moment in the opposite direction of the moment of the task finger (i.e., antagonist). The ring and little fingers are ANTs for the index finger task. The moment arm of ring finger normal force is shorter than that of little finger so the ring and little fingers are, respectively, classified as ANT1 and ANT2. The mechanical advantage indices (MAI) of the ANT1 and ANT2 for the given conditions were calculated using Eq. (6). We also calculated the MAI difference between the fixed and free object prehension conditions using Eq. (7) in order to investigate the effects of the rotational external constraint on static grasping tasks after removing internal constraints

$$MAI^j_i = \left[\sum^{m} (F^{ij} / F^i_{\max}) \Big/ m\right] \times 100\% \tag{6}$$

$$MAI_{residual} = MAI_{fixed} - MAI_{free} \tag{7}$$

where i = {index, middle, ring, and little}, j = {ANT1, ANT2}, and m is the number of variables within each calculation. F^{ij} is a force production by the antagonist (j) during the i finger maximum force task. The calculations were performed on the normal forces only. $MAI_{residual}$ was obtained by subtracting the MAI of the fixed object prehension condition from the MAI of free object prehension condition.

2.5. Statistics

ANOVAs were used with the following factors: finger (the four levels of task fingers: index, middle, ring, and little finger, or two levels: peripheral and central fingers), task (the two levels of prehension tasks: the fixed object and the free object), rank (the three levels of anatomical ranks of fingers: first, second, and third), and ANTAGONIST (two levels of antagonist fingers: ANT1 and ANT2). The factors were chosen based on particular comparisons. Linear regression was employed in order to characterize the relationship between the thumb's normal force and the task-finger's normal force for the fixed and free object prehension tasks. Significance for all statistical tests was set at α = .05.

3. Results

During the free object prehension task, participants held the handle quasi-statically while receiving feedback regarding the real-time angular position of handle. Although only the real-time feedback of angular position was given to the participants, the root-mean-square (RMS) errors of linear positions with respect to all three axes were very small for all tasks (T-task: 0.53 ± 0.13 cm, I-task: 0.51 ± 0.08 cm, M-task: 0.45 ± 0.11 cm, R-task: 0.52 ± 0.08 cm, L-task: 0.45 ± 0.09 cm, TIMRL-task: 0.54 ± 0.11 cm). Substantial force production by non-task fingers was apparent during both fixed and free object prehension (Table 1).

3.1. Finger inter-dependency index (FII)

In general, the FII values of lower fingers (i.e., ring and little fingers) were greater than those of upper fingers (i.e., index and middle fingers) for both fixed and free object conditions. However, the FII values of peripheral fingers (i.e., index and little finger) under the free object condition were greater than those under the fixed object condition (Fig. 2), while the central fingers (i.e., middle and ring) did not show a difference between the two task conditions. These results were confirmed by a two-way repeated-measured ANOVA with the factors finger (four levels) and task (two levels). The effect of the factors and their interaction were statistically significant [finger: $F(3, 27) = 26.380$, $p < .005$; task: $F(1, 9) = 16.03$, $p < .01$; Finger × Task: $F(3, 27) = 6.70$, $p < .01$]. Pair-wise comparisons showed that FII values of the fixed and free object conditions were different in the index and little finger tasks ($p < .01$).

3.2. Proximity index (PXI)

PXI values of the first rank finger was greater than that of the second and third (1st > 3rd > 2nd) during the fixed object prehension. During the free object prehension, however, the PXI of the third was the largest (3rd > 1st > 2nd). The PXI values during the free object prehension were greater than those during the fixed object prehension, particularly in the 2nd and 3rd ranked non-task fingers. These results were supported by a two-way repeated-measured ANOVA with the factors rank and task. The effect of these factors and their interaction were statistically significant [rank: $F(2, 18) = 37.79$, $p < .01$; task: $F(1, 9) = 33.38$, $p < .01$; Rank × Task: $F(2, 18) = 56.23$, $p < .01$]. Pair-wise comparisons showed that PXI values between the two levels of prehension tasks (i.e., fixed and free object) within the second and third rank non-task fingers were significantly different ($p < .01$) (see Fig. 3).

Table 1
Digit normal forces during single-digit MVF tasks under the fixed object and the free object prehension.

Task finger	Fixed object prehension				
	T	I	M	R	L
T	**100.0** ± **0.0**	43.1 ± 8.3	23.1 ± 6.5	28.0 ± 5.1	37.9 ± 5.3
I	61.4 ± 9.2	**100.0** ± **0.0**	15.2 ± 4.2	15.5 ± 3.7	20.5 ± 4.3
M	54.7 ± 7.0	24.0 ± 1.6	**100.0** ± **0.0**	32.0 ± 3.6	10.1 ± 3.2
R	36.4 ± 6.3	14.3 ± 1.7	29.2 ± 2.9	**100.0** ± **0.0**	33.4 ± 6.5
L	30.6 ± 6.2	15.3 ± 1.8	6.2 ± 1.8	46.0 ± 3.9	**100.0** ± **0.0**
TIMRL	**52.0** ± **14.3**	**29.6** ± **7.6**	**31.3** ± **10.9**	**42.9** ± **9.4**	**54.2** ± **12.8**
Task finger	Free object prehension				
	T	I	M	R	L
T	**100.0** ± **0.0**	58.6 ± 3.0	23.8 ± 3.5	38.2 ± 3.1	65.8 ± 6.6
I	100.8 ± 5.6	**100.0** ± **0.0**	12.5 ± 2.3	22.8 ± 3.4	46.6 ± 7.3
M	103.7 ± 7.7	23.9 ± 3.5	**100.0** ± **0.0**	31.1 ± 4.0	17.3 ± 3.3
R	102.9 ± 8.3	21.1 ± 3.0	32.5 ± 2.8	**100.0** ± **0.0**	31.7 ± 5.7
L	102.2 ± 9.0	48.8 ± 5.5	12.3 ± 1.2	37.4 ± 5.9	**100.0** ± **0.0**
TIMRL	**82.9** ± **13.0**	**42.5** ± **4.8**	**28.9** ± **6.2**	**35.5** ± **4.7**	**43.6** ± **6.5**

The values in the table show the digit forces, normalized with respect to the maximum force during the single-digit MVF tasks. The registered values of the multi-digit task (TIMRL-task) were normalized by each single-digit MVF value. The digits investigated during these MVF tasks were the thumb (T), index (I), middle (M), ring (R), and little finger (L). The values above are mean ± SE.

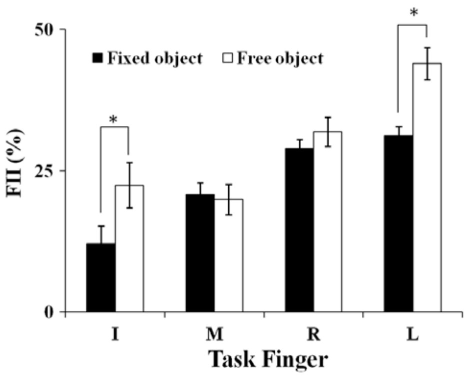

Fig. 2. Finger inter-dependency indices (FII) of task fingers during fixed and free object prehension. The average values across participants are presented with standard error bars. *Represents statistical significance ($p < .05$).

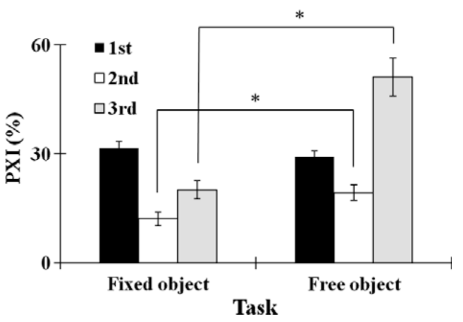

Fig. 3. Proximity indices (PXI) (%) during fixed and free object prehension tasks. The anatomical ranks were defined as the anatomical position of the non-task finger from the task-finger. The 1st is the non-task finger that is the closest to the task finger. The average values across participants are presented with standard error bars. *Represents statistical significance ($p < .05$).

3.3. Mechanical advantage index (MAI)

During the fixed object condition, the MAI of ANT2 was greater than the MAI of ANT1 during the central finger tasks (i.e., middle and ring finger tasks), while the MAI between ANT1 and ANT2 did not show a significant difference in the peripheral finger tasks (i.e., index and little finger tasks) (Fig. 4a). On the contrary, the MAI of ANT2 was greater than ANT1 during the free object prehension peripheral finger tasks, while the MAI of ANT2 is smaller than ANT1 during the central finger tasks (Fig. 4b). A significant difference between the $MAI_{residual}$ of peripheral finger tasks and central finger tasks was observed only in ANT2. However, a significant difference between the $MAI_{residual}$ of ANT1 and ANT2 was identified only in the peripheral finger tasks (Fig. 4c). A two-way repeated-measured ANOVA with the factor finger (two levels: peripheral and central finger tasks) and ANTAGONIST (two levels: ANT1 and ANT2) supported this finding. The effect of the factors and their interaction was statistically significant at $p < .05$ [finger: $F(1, 9) = 43.88$, $p < .01$; antagonist: $F(1, 9) = 31.83$, $p < .01$; Finger × Antagonist: $F(1, 9) = 29.85$, $p < .01$]. Pair-wise comparisons between the MAIs of ANT1 and ANT2 within peripheral finger tasks (Fig. 4c) showed significant differences ($p < .01$).

3.4. Contribution of moment of normal and tangential force to the total moment

During the free object prehension, the percent contribution of the moment of the normal forces (M_n) and the moment of tangential forces (M_t) to the resultant moment (M_{tot}) was almost 50% of each

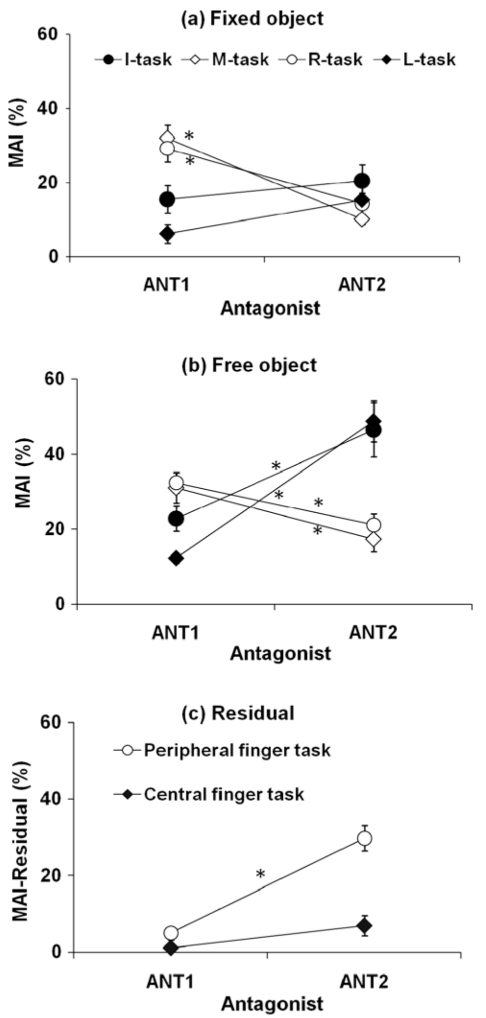

Fig. 4. Mechanical advantage indices (MAI) of ANT1 and 2 at each finger task during (a) fixed object prehension and (b) free object prehension. (c) $MAI_{Residual}$ (=$MAI_{Fixed} - MAI_{Free}$). The average values across participants are presented with standard error bars. *Represents statistical significance ($p < .05$).

(Fig. 5a). The normal and tangential moments worked in opposite directions for all tasks. The two moment components canceled each other out, producing the zero resultant moment during the free object condition (Fig. 5c). On the contrary, the resultant moment ($M_n + M_t$) was not zero during the fixed object prehension (Fig. 5b and c), as the resultant moment was not required to be zero during the fixed object prehension. Specifically, the pronation moment was produced in the thumb, index, and middle finger tasks, whereas the supination moments were generated in the ring and little finger task during the fixed object condition (Fig. 5c). All pair-wise comparisons showed significant differences of the resultant moment between two levels of prehension tasks (i.e., fixed and free object) except for TIM-RL-task ($p < .01$).

3.5. Change of thumb normal force with task-finger normal force

In general, MVF of each task finger during the fixed object prehension was significantly greater than MVF during the free object prehension (e.g., Index: 42.83 ± 2.95 (Fixed) > 22.46 ± 1.87 (Free), Middle:

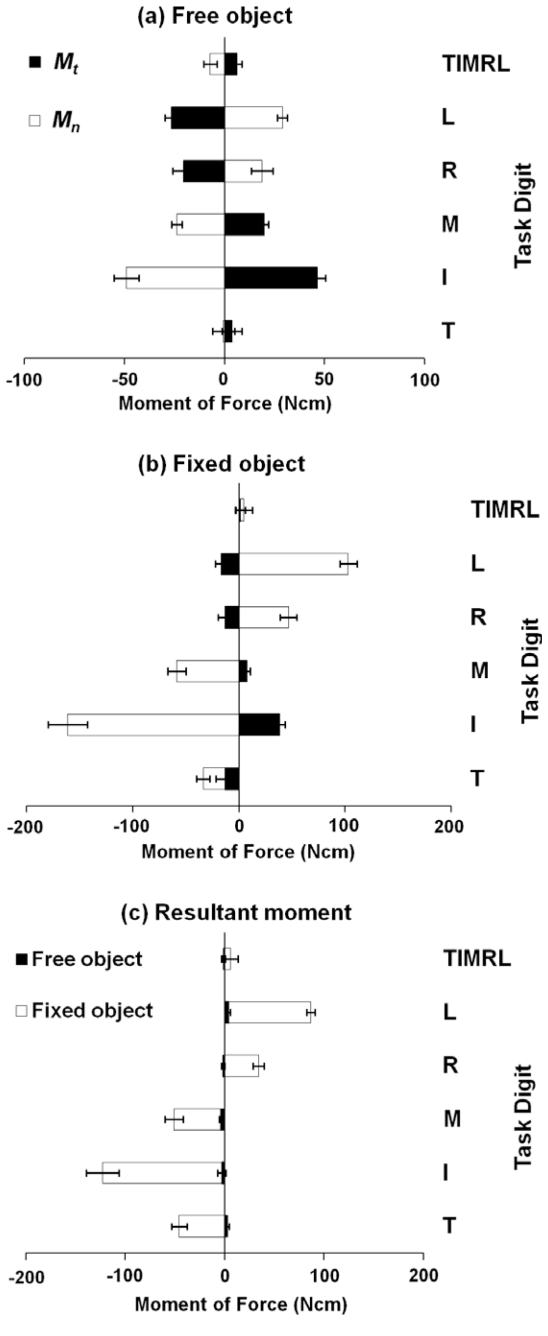

Fig. 5. Contribution of the moments of normal and tangential forces to the resultant moment of force during single-digit and multi-digit MVF tasks under (a) free object and (b) fixed object prehension. Resultant moment of force during single-digit and multi-digit MVF tasks under fixed object and free object prehension (c). Positive and negative values represent the direction of produced moment, clockwise (supination) and counter-clock wise (pronation), respectively. The average values across participants are presented with standard error bars.

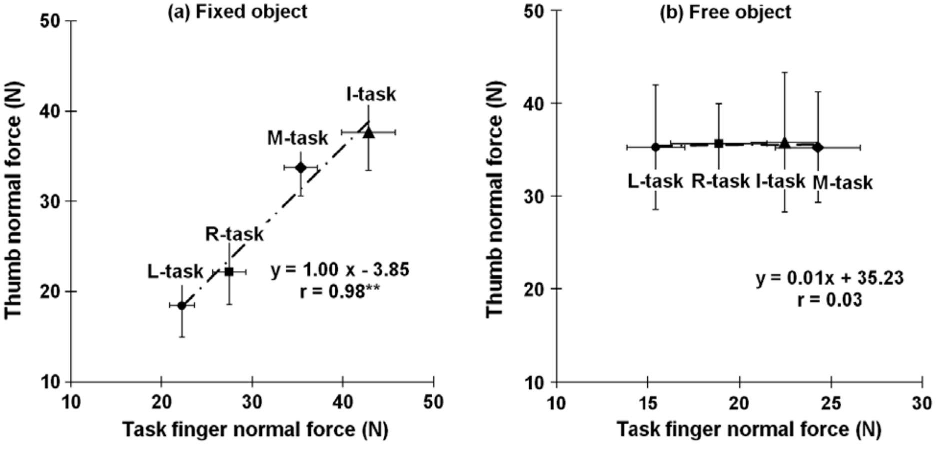

Fig. 6. Relation between thumb normal force (F_n^{th}) and task-finger normal force under (a) the fixed object prehension and (b) the free object prehension. Data averaged across all participants are presented here with standard error bars. (** $p < .01$).

35.34 ± 1.84 > 24.27 ± 2.31, Ring: 27.46 ± 1.85 > 18.88 ± 2.61, and Little: 22.24 ± 1.35 > 15.43 ± 1.59, unit: N, $p < .05$ for all). During the fixed object prehension, the normal force of the thumb as a non-task digit increased linearly with the target finger normal forces (Fig. 6a). In addition, the normal force of the thumb as a non-task digit was the same as normal force of the task fingers in each finger task. During the free object prehension, however, the thumb normal force was quite constant regardless of the magnitude of task-finger force (Fig. 6b). These findings were confirmed by the linear regression analysis. The thumb normal forces were in direct proportion to the task-finger force in the fixed object prehension (slope: 1, $r = .98$), while the slope of regression equation of the free object condition was zero (slope: 0, $r = .03$).

4. Discussion

This study investigated the digit force interactions during single-digit and all-digit maximum normal/grasping force production under a fixed object and a free object prehension conditions. The following topics are addressed in this discussion: (1) the proximity hypothesis vs. mechanical advantage hypothesis, (2) moment control with mechanical constraints, and (3) scaled thumb force with mechanical constraints.

4.1. Proximity hypothesis vs. mechanical advantage hypothesis

Previous studies on finger inter-dependency employed finger pressing tasks (Shinohara, Latash, & Zatsiorsky, 2003; Zatsiorsky et al., 1998) rather than more functional grasping tasks. The main purposes of these previous studies were to examine the finger force interaction caused by the internal constraints such as biomechanical and central constraints (Hager-Ross & Schieber, 2000; Latash et al., 2002; Li, Dun, Harkness, & Brininger, 2004; Zatsiorsky et al., 1998, 2000).

In this study, we employed two prehension tasks, i.e., fixed object and free object prehension, to investigate finger inter-dependency with and without the static rotational constraint. In this study, the fixed object condition was similar to pressing tasks against a vertical surface as opposed to pressing a horizontal surface, which involves the thumb. Olafsdottir and her colleagues reported that indices of digit interaction when the thumb acted in parallel to the fingers were similar to those when the thumb acted in opposition to the fingers (Olafsdottir et al., 2005). The task employed in their study was to press the sensors by digits against a horizontal surface, and it is questionable whether there is a significant difference regarding digit interactions between the pressing task against a vertical surface and a horizontal surface. Although it is still questionable whether the fixed object condition can be qualified as prehension task, we considered it as a prehension task because all hand digits were involved in the tasks and formed the opposition (Naiper, 1956, 1962) in the same way as free object condition. The grasping configuration of the hand during the fixed object condition was designed to be similar to that of free object condition in order to compare the two prehension conditions.

Our assumption was that both internal and external constraints (i.e., static rotational constraint) have influences on the actions of non-task fingers during free object prehension while only the internal constraints affect the non-task fingers' actions during mechanically fixed object prehension. During the fixed object prehension, the external force produced by digits engaging with the handle can be of any magnitude and direction because there was no prescribed condition among finger forces during fixed object prehension (Shim et al., 2004). Supposedly, the force combinations amongst digits would follow the controller's specific principles rather than the mechanical principles during the fixed object condition.

During the fixed object prehension in the current study, it was obvious that the magnitude of non-task-finger force by the neighboring fingers was greater than that of other fingers farther away from the task finger. However, the digit force interaction between digit forces during the free object prehension did not follow the finger force profiles observed in the fixed object prehension. We assume that the CNS strategies for controlling the digit force would alter according to the task mechanics (i.e., mechanical constraints) during the static free object prehension. In other words, the CNS employs an alternative strategy which follows mechanical principles such as force and moment equilibrium for the free object prehension.

We hypothesized that the non-task-finger force profiles follow the mechanical advantage hypothesis during the free object prehension because using mechanical advantage would be the effective way to reduce the total digit force and satisfy the moment equilibrium. Several previous studies considered mechanical advantage as the CNS's primary strategy to control moment of force during prehension (Shim et al., 2004; Zatsiorsky et al., 2002). However, the results of the current study suggest that only peripheral finger tasks (i.e., index and little finger tasks) follow the mechanical advantage hypothesis, whereas the control of central finger tasks (i.e., middle and ring finger tasks) was supported more by the proximity hypothesis. The digit forces during the free object prehension are presumably explained by both the controller's specific principle for governing the redundant hand system and the mechanical principles in order to satisfy task mechanics. Assuming that both internal and external mechanical constraints are linearly superposed, the $MAI_{Residual}$ should follow the mechanical advantage hypothesis. Theoretically, individual finger force is linearly dependent on the mechanical advantage of the individual fingers during the voluntary torque production task (Shim et al., 2005). However, this expectation was only fulfilled in peripheral finger (i.e., index and little finger) tasks. In other words, the mechanical advantage hypothesis as the CNS's strategy for governing force production by non-task fingers does not apply to all finger tasks, and is not linearly independent from other CNS strategies used during the free object prehension task. We assume that the torque demand by the central finger might not reach a sufficient level for the mechanical advantage strategy, resulting in the continued manifestation of the proximity hypothesis in the control of non-task fingers. If this assumption is true, the level of torque demand indicates the borderline where these two strategies intersect. Investigating this borderline would be an interesting future experiment. Furthermore, the mechanical constraints in the current study contain all three subsets of two-dimensional constraints (e.g., horizontal translation, vertical translation, and rotational equilibrium). The effects of different combinations of sub-mechanical constraints and the relationship with internal constraints remain to be explored.

4.2. Moment control with mechanical constraints

Digit normal forces were the primary force components during the tasks in the current study because the task was to produce maximum normal force and tangential force was not required with the counter-balance load. If the gravitational effect of the handle was taken into consideration, the magnitude of tangential force would have been mainly determined by considering the weight of the object. This suggests that the slip prevention associated with relationships between normal and tangential forces could be a meaningful issue (Flanagan, Burstedt, & Johansson, 1999; Johansson, Backlin, & Burstedt, 1999; Pataky, Latash, & Zatsiorsky, 2004; Westling & Johansson, 1984), and that the interpretation of tangential force production should include the force direction in terms of object weight (Kinoshita, Backstrom, Flanagan, & Johansson, 1997; Westling & Johansson, 1984), slip prevention (Wheat, Salo, & Goodwin, 2004; Zatsiorsky, Gao, & Latash, 2003), and moment equilibrium (Gao, Latash, & Zatsiorsky, 2005b; Latash, Shim, Gao, & Zatsiorsky, 2004; Shim et al., 2005; Zatsiorsky et al., 2002). The relationship between grasp force (i.e., normal force) and load force (i.e., tangential force) was linear (Kinoshita, Kawai, & Ikuta, 1995; Monzee, Lamarre, & Smith, 2003) in cases where the load force is a necessary force component during the task. In the present study, however, the task was to produce single-digit or all-digit normal forces, and the tangential force was necessary in neither the fixed object nor free object prehension conditions. This suggests that the tangential force does not have a mechanical reason to be coupled with the normal force. The approaches to answering the role of tangential force in the current study are different from the previous studies. During data analysis, it became clear that the direction of moment of resultant tangential forces ($\sum M_t$) was opposite to that of the resultant of normal force ($\sum M_n$) even though the ratios of the moment of normal and tangential force were varied with the experimental conditions. We then investigated how the CNS controls an inevitable tangential force production. The results showed that the percent distributions of normal and tangential force were almost 50% for both components of force throughout all task digits during the free object condition. There are two possible ways to satisfy the moment equilibrium regarding normal and tangential force control for the free object prehension in the current experiment. The first would be to minimize the sum of the moments of the normal forces (Flanagan et al., 1999). The second would be to produce the opposite directional moment of tangential forces to the moment of normal force (Zatsiorsky et al., 2003). Considering the results of the normal and tangential force contributions to the resultant moment (Fig. 5), it seems that the CNS utilizes both strategies to maintain the moment equilibrium. The first strategy for moment equilibrium (i.e., the minimization of resultant moment of normal force) can be explained by the mechanical advantage hypothesis. Because the peripheral fingers (e.g., index and little finger) showed the greater *MAI* (i.e., greater non-task fingers normal forces) than the central fingers did and the two peripheral fingers' normal forces produced opposite directional moments, the moment of resultant normal forces during the free object prehension could be less than the moment of resultant normal forces during fixed object prehension. However, the minimization of the moment of resultant normal forces employing the mechanical advantage hypothesis was not enough to produce zero resultant moment of forces. Therefore, the CNS also employed a second strategy for moment equilibrium (i.e., the production of a force of the same magnitude but working in the opposite direction of the tangential force's moment). This finding coincided with the fact that one half of the torque was exerted by the tangential force during the free object prehension in a previous study (Zatsiorsky et al., 2003). In the analysis, we only considered the normal forces of individual digits to compute the mechanical advantage index. The lever arms for the tangential forces of individual digits are the same, meaning that there was no difference on the mechanical advantage of tangential force production among digits.

Mechanically speaking, TIMRL- and T-tasks can be considered a pressing task regarding the action of fingers. In comparing the components of force production seen during the fixed object prehension, the ratio of non-task fingers' normal forces to the tangential force under the free object condition was greater than under the fixed object condition (Fig. 5a and b). The magnitudes of moments either of normal or of tangential force in the TIMRL- and T-tasks were smaller than those of any other tasks. We can infer that the principle of the minimization of the secondary moment, the sharing pattern between finger forces as a way to minimize secondary moments like the pronation and supination moments (Li, Zatsiorsky, Li, Danion, & Latash, 2001; Zatsiorsky et al., 2000), would be valid during prehension. Nevertheless, it is still questionable whether the principle of the minimization of secondary moment is valid during the prehension task when that task includes a gravitational effect.

4.3. Scaled thumb force with mechanical constraint

The flexor pollicis longus (FPL) muscle is a flexor of the thumb, and is considered an anatomically independent muscle. This implies that the FPL does not contribute to other fingers' movements (Brand & Hollister, 1999). In other words, it is assumed that there is no known muscle-tendon connection between thumb and other fingers for the flexion. However, the recent investigation by Yu and colleagues revealed the neural coupling between FPL and the flexor of the index finger by showing peripheral force transfer to the index finger (Yu, Kilbreath, Fitzpatrick, & Gandevia, 2007). In this study, there was an evident relationship between thumb enslaving force and task-finger force. Indeed, the force of the thumb as a non-task digit was increased with the task-finger forces under the fixed object prehension. Thumb forces were constant regardless of the task-finger forces during the free object prehension (Fig. 6). It is reasonable to interpret this as evidence that the interaction between the thumb and fingers is caused mainly by the central constraints, not the anatomical connection. Earlier studies found in-phase changes between the thumb and finger forces in the frequency domain during prehension tasks (Rearick & Santello, 2002). Combining this previous finding with our results, we can conclude that the interaction between the thumb and the finger forces is explained by the phase-relationship (in-phase) and the scaled amplitude, where amplitude is the scaled finger force incorporating the thumb force during the fixed object prehension. Presumably, these two phenomena are caused by the central constraint. However, when the mechanical constraints were imposed in the hand-held object system, the magnitudes of finger normal forces were not scaled, but were instead limited due to the task constraint (i.e., normal force constraint). It was shown that the thumb normal forces were constant across all single-finger MVF tasks (i.e., I-, M-, R-, and L-tasks), meaning that total normal force produced by all fingers was the same across all single-finger MVF tasks for the free object condition. Therefore, the thumb normal force seems to be a limiting factor for the force production in task fingers during free object prehension. During free object prehension, the CNS considers task mechanics so that the interaction strategy between the thumb and the fingers is different from the strategy employed in the fixed object prehension.

The thumb forces as non-task digits were similar to the thumb maximal force during the free object prehension. This implies that the thumb force remains the same for all task finger conditions in much the same way the maximal force production ability does under the free object condition, whereas finger forces were shared within the thumb force magnitude considering the force and moment constraints. These interactions between the thumb and finger forces could be explained solely by the central constraints. Previous studies performed by Schieber and colleagues have revealed that each set of muscles is not controlled from a somatotopically distinct region of the primary motor cortex (M1) (Schieber, 1996). More recent studies have revealed that the inter-dependency between the thumb and fingers was an evident phenomenon of the human digits' actions (Olafsdottir et al., 2005; Yu et al., 2007). The current study also supports this view. This suggests that an independent set of flexor and extensor muscles for each digit does not fully account for digit movements. Even the somatotopy of M1 is not spatially segregated; rather, it encompasses several spatially overlapped M1 neurons (Dechent & Frahm, 2003; Schieber, 2001).

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