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DIGIT FORCE ADJUSTMENTS DURING FINGER ADDITION/ REMOVAL IN MULTI-DIGIT PREHENSION

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Abstract

We explored adjustments in multi-digit coordinated action on a hand-held object with finger addition and removal. The subjects ($n = 7$) kept a vertically oriented handle at rest using a prismatic grasp as if holding a glass of liquid and then either added one finger to the grasp—the index (I) or little (L) finger—or removed one finger. Three external torques were applied on the apparatus: clockwise, counterclockwise, and no torque. The individual digit forces and moments were recorded with 6-component sensors. The change in grasping force depended on the function of the manipulated finger, i.e. on whether the finger resisted external torque (torque agonist) or assisted it (torque antagonist). There was a significant increase of the grasping force when an antagonist was added or when an agonist was removed. These force increases were not necessary for slipping prevention: the normal forces prior to the manipulation were large enough to prevent slipping. All other finger manipulations exhibited no significant change in the grip force, except for the antagonist removal during the supination efforts (after removing the I finger the grasping force decreased). In contrast, the changes in the tangential force depended on the manipulated finger, not on the finger function with respect to external torque. There was a significant thumb force increase when the I finger was added or when the L finger was removed; opposite changes were seen when the L finger was added or the I finger was removed. The changes of the virtual finger (VF) tangential force were equal and opposite to the thumb tangential force alterations; these opposite changes caused changes in the moments these forces generated. The changes in the moments of the tangential forces were counterbalanced by the opposite changes in the moments of normal forces such that the total moment remained constant and the handle orientation was maintained. At the level of individual finger (IF) forces two strategies of error compensation were found: (a) *local error compensation* - the opposite action of the neighboring finger, i.e. force decrease in response to a force increase (finger addition), and vice versa, and (b) *distant error compensation* - similar action by a finger that is a torque antagonist to the manipulated finger. During the transient periods, the changes in the thumb and VF forces were simultaneous and equal in magnitude. The normal forces increased or decreased concurrently while the changes in the tangential forces were opposite in direction. The data support the existence of chain effects in the digit force adjustments to finger addition or removal. We conclude that the digit force adjustments during the object manipulation are controlled mainly in a feed-forward manner. The obtained data agree with the principle of superposition reported previously. The findings agree with earlier reports on the limited ability of CNS to organize synergies at two levels of a control hierarchy simultaneously.

Keywords

prehension; grasping; grasp stability; error compensation; synergy; chain effects

INTRODUCTION

During some multi-finger prehension tasks, the actors alter the number of fingers touching the object; for example, when playing a wind instrument. Because equilibrium has to be maintained (anyone who played a wind instrument would agree that maintaining the instrument steady is a difficult task), all of the digit forces should be precisely coordinated. In particular, the forces have to satisfy mechanical equilibrium constraints. There are also biological constraints that should be either overridden or satisfied (these constraints are considered later). To our knowledge, no studies have addressed effects of removing or adding a finger during grasping; hence, this is an exploratory study.

We focused on the prismatic grasp when a person keeps a vertically oriented handle at rest, as if holding a glass of liquid (Figure 1). In such a grasp, the thumb and the fingers oppose each other. Control of the prismatic grasp is frequently considered as being based on a two-level hierarchy: at the upper level, the task is shared between the thumb and a virtual finger (VF), an imagined finger that produces the same mechanical effect (wrench) as several fingers combined (Arbib et al. 1985; Iberall 1987; Santello and Soechting, 2000); at the lower level, action of the VF is shared among the actual fingers. During the performance, there are four mechanical constraints that must be satisfied: (i) no-slip constraint: the normal forces of the thumb and VF should be sufficiently large to prevent slipping (Johansson and Westling 1984; Latash 2000; Kinoshita et al. 1996; Burstedt et al. 1999; Flanagan and Johansson 2002); (ii) the sum of the thumb and VF normal forces should equal zero; (iii) the tangential forces of the thumb and VF should equal the supported load; and (iv) the moment of force generated by the performer should be equal and opposite to the external torque acting on the handle.

During multi-finger prehension the finger force control follows the principle of superposition. The principle was first suggested in robotics (Arimoto et al. 2001) and then confirmed for human grasping (Zatsiorsky et al. 2003; Zatsiorsky et al. 2004; Pataky et al. 2004a; Latash et al. 2004; Shim et al. 2005a). According to the principle, the central controller employs two commands for grasping control: (1) grasp the object stronger or weaker to prevent slipping, and (2) prevent tilting of the object. The summation of these two commands produces the final grasp. Following the principle, the digit forces are organized into two subgroups. The correlation across trials between the variables from the same group is close to plus or minus one, while the correlation between the variables from different subgroups is close to zero. The variables are said to form two null spaces: the forces in each group co-vary to satisfy equilibrium constraints and do not perturb the object equilibrium. Such a grasp control involves so-called chain effects: sequences of local cause-effect adjustments necessitated by the task mechanics (Zatsiorsky et al. 2003; Zatsiorsky et al., 2003; Shim et al., 2003 and 2005a).

Biological constraints on the finger forces in the tasks involving addition or removal of a finger were previously considered in the framework of “the principle of error compensation” (Latash et al. 1998; Shinohara et al. 2003). The error compensation is an essential attribute of the movement synergies in general and has been observed in many motor tasks (reviewed in Turvey 2007). In particular, multi-finger tasks changes in the force generated by one of the fingers are compensated by force changes of other fingers (Latash et al. 1998; Shinohara et al. 2003). The principle was confirmed for tapping tasks (Latash et al. 1998) and pressing tasks (Li et al. 2003). In the former study subjects pressed at about 30% of the maximal contraction force with three fingers (index, middle, and ring) acting in parallel. Then, they performed a series of taps with one of the fingers. The non-tapping fingers changed their force production – without a time delay – with the changes in the force by the tapping finger. The force changes in the non-tapping fingers compensated for the expected variation in the total finger force during tapping. In the latter experiment the subjects produced maximal voluntary contraction (MVC) with explicitly instructed (“master”) fingers. After reaching maximal force with a set of master

fingers, the subjects added/removed one master finger while continuing to produce the MVC with the new group of master fingers. A significant increase in the forces of remaining master fingers was observed after finger removal and a close-to-significant drop in the forces of previously recruited master fingers was observed after finger addition. On the whole, the data supported a principle of error compensation, a major principle of synergy organization during motor tasks performed by a redundant set of effectors. The validity of the principle for the finger pressing tasks was also confirmed in several studies performed using the framework of the uncontrolled manifold (UCM) hypothesis: a negative co-variation of the individual finger forces leading to the stabilization of the total force output has been observed (Shinohara et al. 2003; Shinohara et al. 2004; Shim et al. 2003b; Shim et al. 2005).

In the present study we are interested in the manifestation of the principle of error compensation during prehension – when a subject holds a handheld object at rest and then adds or removes one finger to/from the grasp – as well as in three other questions:

Question 1 – how does the central controller adjust digit forces to maintain the object equilibrium? Consider as an example a 4-to-3 task when the performer holds a handle using four fingers and then removes one finger, e.g. the index (I) finger. We should expect that after the removal the normal forces of the middle (M), ring (R) and little (L) finger increase. Such an expected digit force adjustment follows from the principle of error compensation mentioned previously as well as from the mechanical necessity to prevent object slipping. However, removal of the I finger will perturb the rotational equilibrium of the handle. If the M, R and L forces simply increase to compensate for decreased VF force, the handle will rotate clockwise. To prevent the tilt the central controller has many options that can be viewed as belonging to one of two groups: (a) the equilibrium is maintained solely by redistributing the normal forces among the fingers, in such a strategy the moment of the normal force does not change; and (b) the moment of the normal forces changes but it is countered by a properly modified moment of the tangential forces. In the first case, the equilibrium is maintained solely by the synergic force adjustments at the level of normal forces while in the second case the tangential force adjustments are also employed to keep the object at rotational equilibrium. Note that both options satisfy the task mechanics: each of them potentially can be used. We were interested in whether option (a) or option (b) is used by the neural controller. We were also interested in whether the thumb and VF force changes depend on finger function in the torque production (on whether the finger resists or assists an external torque), or on the finger itself.

Question 2 – are the finger force adjustments in prehension controlled in a feed-forward manner? Simultaneous synchronous force changes of the manipulated and non-manipulated fingers will support this conjecture while substantial time delays in the finger force adjustments will speak against it.

Question 3 – we already know from previous studies that grasping patterns during static prehension support the principle of superposition (Zatsiorsky et al. 2004). When a finger is added or removed, are the forces still organized according to this principle? The latter question can be reformulated as follows: are digit forces during finger manipulation organized into two subgroups associated with the slip and tilt prevention, respectively?

METHODS

Seven male subjects with the age = 27.6 ± 4.3 yrs (mean $\pm$ STD), height = 177.7 ± 3.8 cm, weight = 82.6 ± 12.8 kg, hand width = 9.4 ± 0.4 cm and hand length –measured from middle fingertip to distal crease while the hand was extended – 19.1 ± 1.2 cm, participated in this study. Each subject was identified as right-handed by the reported daily use of their hands. No history of neuropathies or traumas to the upper extremities was reported by any subject. No

females were included in the study because hands of females are usual smaller than those of males and testing the both genders with the handle of the same size could distort the experimental results. All subjects gave informed consent in accordance with the procedures approved by the Office of Research Protections of The Pennsylvania State University.

Apparatus

Five six-component force/moment sensors (Nano-17, ATI Industrial Automation, Garner, NC, USA) were attached to an aluminum handle such that four sensors were on one side and the remaining sensor on the other, Figure 1 (top panel). The centers of all five sensors were in one plane (the grasp plane). The vertical distance between adjacent sensors, for the fingers, was 30 mm. The sensors were fixed to the handle such that the vertical distance between the handle center and the middle finger sensor, being above the handle's center, was 15 mm. The distance between the handle's center and the ring finger sensor, being below the handle's vertical center, was also 15 mm. The position of the index finger sensor followed the arrangement of sensors; the same paradigm is followed for the little finger sensor. The thumb sensor was located at the vertical midpoint of the handle. Sandpaper (100-grit) was attached to the surface of each sensor such that the fingertip pressed against the sandpaper. The horizontal distance between the surface of the thumb sensor and finger sensors was 73 mm. An aluminum beam was attached to the bottom of the handle and orientated in the medio-lateral direction; i.e. a vector normal to the surface of any sensor was parallel to the beam. A 3-D position sensor (MT9-B, Xsens Technologies, Netherlands, weight = 35 g) was attached to the handle facing away from the subject. A 2-D bubble-level was fixed to the top of the handle for orientation feedback to the subject.

Each sensor produced six voltages, one for each degree of freedom at the sensor (3 forces and 3 moments of force with respect to the sensor centers). The voltages were multiplied by a calibration matrix to eliminate cross-talk between the channels and the three forces and moments produced at the sensor were recorded. A computer algorithm (Labview, National Instruments, Austin, TX, USA) was written to collect and analyze the signals. The 30 signals were each sampled at 200 Hz with a 16-bit analogue-digital converter (PCI-6033e, National Instruments, Austin, TX, USA) and stored in a Dell desktop computer (Dell Inc., Round Rock, Texas).

Procedure

The subjects were first instructed about the experimental procedure and the equipment. In order to normalize the fingertip conditions of each subject, an alcohol pad was lightly rubbed across each fingertip surface.

The subjects sat on a chair and the forearm was fixed to a table next the chair. A custom mold was created for each subject from a Kay-Splint material (Sammons Preston, Bolingbrook, IL, USA). The material was heated in water until pliable, patted dry and –when at a comfortable temperature – fitted around the subject's right arm such that it covered the arm from 1/3 distally from the elbow to about 1/2 the length of the metacarpals. During fitting, the subject was asked to grasp an unloaded handle (the beam was perpendicular to the antero-posterior axis) so the mold would form a tight fit around the wrist and hand. A layer of foam – for comfort purposes – was placed on top of the subjects' arm and Velcro straps were wrapped around the mold and foam to secure them to the subject. The chair was adjusted vertically and horizontally such that the right shoulder was in approximately 45° of abduction in the frontal plane and 45° of flexion in the sagittal plane while the forearm was resting on a table; the elbow was also approximately at 45° of flexion such that the forearm was aligned parallel to the antero-posterior axis (Figure 1, bottom panel). The handle was suspended by safety lines; it remained suspended until the subjects grasped the object at the beginning of each trial. During a trial, the subjects grasped

the handle with the right hand such that the fingertips were placed approximately at the centers of each sensor. No hyperextension at any of the phalangeal joints was allowed. During the trial the hand and the forearm were both horizontally oriented and the beam attached to the handle was roughly aligned with the medio-lateral axis. When the computer finished recording data, the subjects replaced the handle to the safety lines at the end of each trial.

A load of 0.548 kg was attached to the beam at three different positions (+8.0, 0.0, -8.0 cm) to produce three different external torques on the apparatus: clockwise (CW), counterclockwise (CCW) and no torque (ZERO) respectively. The torque magnitude with respect to the handle center was ± 0.43 Nm. The entire apparatus weighed approximately 10.9 N. During the trials, the subjects were instructed to hold the handle at rest trying to maintain the bubble at the center of the level while exerting minimal grasping forces. By successfully completing this task, the subject “maintains equilibrium”. The subject is then asked to complete a finger addition task – going from a thumb and three-finger grasp to a thumb and four-finger grasp (the 3-to-4 task) – or a finger removal task – going from a thumb and four-finger grasp to a thumb and three-finger grasp (the 4-to-3 task).

The load was fixed in one of the above mentioned torque configurations (CW, CCW, ZERO) and two trials of finger addition and two trials of finger removal for each finger (index-I, middle- M, ring-R, little- L) were performed for a total of 48 trials per subject; however, the outcome of only the I and L finger manipulations are reported in this paper. To prevent the handle from tilting, the subjects exerted pronation efforts (PRO) in the CW tasks and supination efforts (SUP) in the CCW tasks – throughout the rest of the paper we will use the PRO and SUP nomenclature. The PRO torques will be considered positive and the SUP torques negative. When an external load was placed on the bar, the fingers became torque-agonists or -antagonists. During PRO tasks, the I and M fingers were torque agonists – they resisted the external torque –and the M and L fingers were torque-antagonists – they assisted the external torque. During SUP tasks, the roles of the fingers reversed. The order of the moment presentation was random and the trials within each moment configuration were randomized as well. When the subjects were holding the handle such that the bubble was at the center of the level, data recording started. The data were recorded at a sampling frequency of 200 s^{-1} for 8 seconds. Rest periods of at least 30 seconds were given between the trials and at least 3 minutes of rest between torque configurations.

The analysis was conducted with Matlab (Natick, MA, USA) algorithms: the data were low-pass filtered at 10Hz in both directions by a 4th order Butterworth filter. The data were aligned via the time the instructed finger was removed from the sensor or added to the sensor. The instant a finger was added or removed was determined as its force went below (finger removal) or above (finger addition) a threshold value of 0.1 N. Totally, 1100 data samples were analyzed; 549 samples before the finger manipulation and 550 samples during and after the manipulation. To obtain steady-state values, the data were averaged for 1 second during the time periods 0.75–1.75s and 4.25–5.25s with respect to the threshold time.

Modeling

The model is similar to what Zatsiorsky et al. (2003) used. Think of a glass filled with fluid, which is grasped by the fingertips and held in a static state. For the glass to be at rest, the sum of all forces and moments should be zero, therefore the three following requirements must be satisfied:

1. The sum of the normal forces must equal zero: the normal forces of the thumb and the sum of the individual fingers (F_{VP}^n) are equal and opposite of each other, Equation (1).

$$F_{th}^n = F_i^n + F_m^n + F_r^n + F_l^n = \sum_{f=1}^4 F_f^n = F_{VF}^n \quad (1)$$

2. The sum of the tangential forces must equal the weight (W) of the handle, Equation (2).

$$F_{th}^t + F_i^t + F_m^t + F_r^t + F_l^t = W \quad (2)$$

3. The total moment on the handle must equal zero: the moment created by the digits equals the external torque, Equation (3).

$$M = \overbrace{F_{th}^n d_{th} - F_i^n d_i - F_m^n d_m + F_r^n d_r + F_l^n d_l}^{\text{Moment of the normal forces} \equiv M^n} - \overbrace{F_{th}^t k + F_i^t k + F_m^t k + F_r^t k + F_l^t k}^{\text{Moment of the tangential forces} \equiv M^t} \quad (3)$$

where the n and t represent normal and tangential forces and the i , m , r and l represent the index, middle, ring and little fingers, respectively; d stands for the vertical distance from the center of the handle to the point of force application on the digit sensor; k stands for the horizontal distance from the center of the handle (height of the sensor plus half of the width of the handle). The rightward and upward directions were chosen as positive. Hence the thumb normal forces were considered positive and the fingers forces negative.

To compute the moments of the normal forces mentioned in equation (3) the following procedure was used. During the performance the subjects do not exert forces exactly at the sensor centers. This creates a moment at the sensor M_z^i (moment about the z axis; the z -axis is approximately parallel to the antero-posterior axis, refer to Figure 2); thus the moment arm for the normal force applied at each finger, and thumb, needed to be calculated as such, Equation (4).

$$d_i = \frac{M_z^i}{F_i^n} + A_i, i=1,2,3 \text{ and } 4 \text{ for the fingers and } 5 \text{ for the thumb} \quad (4)$$

where M_z^i is the moment created by the i^{th} finger or thumb at the sensor and F_i^n is the normal force created by the i^{th} finger. A_i is the fixed distance between the handle's center and the center of the i^{th} sensor. These data were used to compute the moment arms of the digit forces, d_i .

The couple arm is another variable that can be manipulated during the trials: computed as the distance between the two points of normal force application by the VF and thumb. The Varignon theorem of classical mechanics was used to calculate the VF and thumb moment arms with respect to the handle's center of mass; then the distances were subtracted from each other to calculate the couple arm, D , Equation (5)

$$D = \frac{\sum_{f=1}^4 F_f^n d_f}{\sum_{f=1}^4 F_f^n} - \frac{M_z^{th}}{F_{th}^n} \quad (5)$$

where F_f^n is the normal force of the finger f and d_f is the moment arm of the same finger; also, F_{th}^n is the normal force of the thumb and M_z^{th} is the moment created at the thumb fingertip about

the z-axis. The couple arm can be seen as a projected vertical distance between the points of application of the VF and thumb normal forces.

To determine whether there was a significant increase or decrease in the steady-state thumb and VF forces a one-way ANOVA with the factor PERTURBATION (2 levels: before, after) was performed for each torque condition and finger manipulation on the digit forces and moments. Note that the question of interest was how a specific finger manipulation (finger addition or removal) at a specific torque condition, not a finger manipulation in general, affects the thumb and VF normal and tangential forces. Hence no Bonferroni correction was required. We were not interested in how the torque or the manipulated finger affected the thumb and VF forces prior to the perturbation, so these factors were not included in the model. Statistical significance was tested at the level of 0.05.

The same method of statistics used for the thumb and VF was applied to the individual fingers (I, M, R and L) to check if there were any significant changes in their normal force and tangential force. A one-way repeated measure ANOVA with the factor PERTURBATION (before, after) was performed for each finger, torque, and manipulation condition.

RESULTS

The results are presented in the following sequence. First, we describe the findings for the VF level, i.e. the VF and thumb forces and moments only. The steady-state changes are described first and the transition periods afterwards. Then the data for the individual finger forces are presented.

The VF level

Steady State

Normal forces: In all cases the thumb normal force equaled the VF normal force, as it should be expected from equation (1). We will call collectively the thumb and VF force the *grasping force*.

The data are best explained in terms of torque agonist and antagonist (recall – the I finger is a torque agonist during PRO efforts and an antagonist during SUP efforts; for the L finger the action is opposite). The change in grasping force with finger addition/removal depended on the finger function, i.e. on whether the manipulated finger was a torque agonist or antagonist in the task, Table 1-a. There was a significant increase when an antagonist was added (PRO-L, $p=0.028$; SUP-I, $p=0.006$) and when an agonist was removed (PRO-I, $p=0.003$ and SUP-L, $p=0.008$). These force increases were not necessary for slipping prevention: the normal forces prior to the manipulation were large enough to prevent slipping. All other finger manipulations exhibited no significant change in grasping force, except for the antagonist removal during the SUP efforts (after removing the I finger the grasping force decreased by 1.60 ± 0.44 N; $p=0.011$).

During the zero torque task, the way the finger was manipulated (addition or removal) influenced changes in the thumb and VF normal force. In the 3-to-4 tasks the grasping force significantly increased (I – $p=0.030$, L – $p=0.007$), Table 1-b. The three non-manipulated fingers did not compensate fully for the force increase created by the added finger. Similarly to the cases described above the grasping force increases were not mechanically necessary for slipping prevention. During the 4-to-3 task there were no significant changes in the grip force: the three non-manipulated fingers increased the force to compensate for the grip force drop due to the finger removing. Hence, in the zero torque tasks the principle of error compensation reported previously for the finger pressing and tapping was valid for the finger removal but not for finger addition.

Tangential forces: In all cases the sum of the thumb and VF tangential forces was very close to the weight of the apparatus, as it should be expected from equation (2). In contrast to the normal force changes, the change in the tangential forces of the thumb and VF depended on which finger was manipulated, not on the finger function in the task – whether the finger served as torque agonist or antagonist.

Addition of the I finger resulted in an increase of the thumb force (and hence in the decrease of the VF force) in all torque conditions (Table 2-a). Opposite changes were observed after the I finger removal: the thumb tangential force decreased (and VF tangential force increased) significantly in all torque conditions (PRO – $p=0.001$, ZERO – $p=0.007$, SUP – $p=0.019$).

The manipulation of the L finger induced the changes opposite to those seen after the I finger manipulation. In particular, when the L finger was removed, the thumb tangential force increased significantly (PRO – $p=0.001$, ZERO – $p=0.001$, SUP – $p=0.001$), Table 2-b. The L addition resulted in a decrease in the thumb tangential force; however the level of statistical significance was reached only during the ZERO ($p=0.002$) and SUP ($p=0.002$) efforts.

The changes in the VF tangential forces following the I finger manipulation were counter-intuitive: addition of the I finger resulted in a decrease of the VF force while the I finger removal resulted in a VF force increase. For the L finger manipulations, the changes were opposite.

Tilt prevention: Because the sum of the thumb and VF tangential forces stayed constant, an increase/decrease of one force was accompanied by a concurrent decrease/increase of the second force and hence changed the moment that these forces generated (Table 3). After the I finger addition or the L finger removal, the changes of the moment of the tangential forces were negative, i.e. the moment in the PRO direction decreased (or increased in the SUP direction), Table 3. Alternatively, after the I finger removal or the L finger addition the moment changes were in the positive (pronation) direction. In one condition, the L finger removal in the CW/PRO task, the changes did not reach the level of statistical significance. The data presented in Tables 2 and 3 match each other well, as it should be from Equation (3). All positive changes in Table 2 (with the plus sign) correspond to the negative changes in Table 3 (with the minus sign), while all the ‘minus changes’ in Table 2 correspond to the ‘plus changes’ in Table 3.

The changes in the moment of the tangential forces were counterbalanced by the opposite changes in the moment of normal forces such that the total moment remained constant and the vertical handle orientation was maintained (to avoid the duplication with Table 3, these data are not presented here). Note that, in contrast to the tangential force changes, the normal force changes did not correlate with the changes in the moments of force, cf. Table 1 with Table 3.

Transition Period—The transition period is defined as the interval between the two steady-states.

VF and thumb forces: During the transition period, changes in forces by the thumb and VF were simultaneous and equal in magnitude. The normal forces increased or decreased concurrently while the changes in the tangential forces were opposite in direction – for an example, see Figure 2. As a result the equilibrium requirements represented by equations (1) and (2) were always satisfied.

The opposite changes of the thumb and VF tangential forces induced changes in the moment of the tangential forces. In the steady-state after the transition period, these changes were compensated by matching changes of the moment of normal forces but during the transition

period the total moment deviated from the nominal values by more than 0.1 Nm in 12 cases of 84 (the complete statistics are presented later in the text.).

To characterize the quality of equilibrium during the transition, the correlation between the normal forces at the thumb and VF was computed as well as the correlation between the tangential forces of the thumb and VF. For the normal force magnitudes, out of all instances (subjects and finger manipulation, 84 totally): 78 (92.8%) had Pearson coefficients above 0.95 (highly correlated), 3 were between 0.80 and 0.95 (moderately correlated), 1 was below 0.80 (poorly correlated). The low correlation values were observed for the trials where the finger force changes were small, below 1.0 N. In two cases the correlations were not recorded due to very small changes in the forces that could not be recognized by the algorithm. For the tangential force magnitudes, out of all instances: 53 had coefficients minus 0.95 or higher, 15 were between minus 0.80 and minus 0.95, 9 were below 0.80, and 7 were not recorded due to the small force changes.

In all the cases the thumb and VF force changes started simultaneously, without a visible time delay. In a majority of cases the thumb-VF force relations were close to a straight line; however, there were cases when the thumb-VF force curves deviated from the straight line or had 'loops' (like at the upper right part of the curve in Figure 3). One possibility is that these deviations from the straight-line point-to-point transitions are indicative of sensory corrections during the performance.

To determine the reason behind these corrections, we calculated the standard deviations of the performance variables (total normal and tangential force and total moment) during the transition periods. A hypothesis was that if the above variables stay put the central controller has no reason to intervene and make corrections. For the standard deviations of the total normal force (N), in 59 cases the values were equal to or below 0.10 N, in 21 cases they were between 0.10 and 0.20 N, and in 4 cases they were equal to or above 0.20; 0.40 N was the highest value. Hence, in 80 cases out of 84 (95.2%) the standard deviation of total normal force acting on the handle was below 0.2 N. For the standard deviations of the total tangential force (N), in 45 cases the values were equal to or below 0.10 N, in 30 cases they were between 0.10 and 0.20 N, and in 9 cases they were greater than or equal to 0.20 N; 0.34 N was the highest recorded value. Thus, the tangential force acting on the handle during the transient period did not deviate more than for 0.2 N (standard deviation) in 75 cases of 84 (89.2%). Note that 0.2 N is less than 2% of the weight of the handle. Finally, for the standard deviations of the total moment of force (Nm), in 72 cases the values were equal to or below 0.10 Nm, in 9 cases they were between 0.10 and 0.20 Nm, and in 3 cases they were equal to or above 0.20 Nm; the highest recorded value was 0.32 Nm. While the forces, measured in newtons, and the moments, measured in newton-meters, cannot be immediately compared, for the subjects the moment of force deviation of 0.2 Nm was perceived as a much larger value than the force deviation of 0.2 N. At the 10.9 N weight of the entire assembly the change of the load by 0.2 N would be almost imperceptible, while resisting an external torque of 0.2 Nm requires substantial muscular efforts. The deviation of 0.2 Nm equals almost 50% of the external torque exerted on the handle (± 0.43 Nm). To sum up, during the transient periods the resultant horizontal and vertical forces exerted on the objects did not vary much while the variations in the moment of force were more substantial. It seems that during the transition period the main challenge is the tilt prevention while the handle stabilization in the horizontal and vertical directions is achieved more easily.

The IF level

In what follows the changes in the forces of the manipulated fingers are not discussed (due to the triviality of the results) but they are still presented in the tables.

Normal forces—When a finger is added or removed, the moment of normal forces exerted on the handle changes. Because torque agonist fingers exert larger forces than the fingers that are torque antagonists, the perturbation of the moment was larger when an agonist finger was manipulated. The nominal value of the M^n can be restored by two mechanisms:

- A. By the symmetric action of a finger that is a torque antagonist for the manipulated finger, e.g. if the I finger is added and generates an additional moment on the handle, this extra-moment can be compensated by an increased force of the L finger; correspondingly the I removal should be accompanied by a force decrease of the L finger. The same is valid for any manipulation of the L finger. We will call this mechanism *distant error compensation*.
- B. By the opposite action of the neighboring finger, i.e. when the I finger is added, to maintain the same moment on the handle as prior to the manipulation, the M finger may decrease its force; the same mechanism applies to the I finger removal and the L finger manipulation. We will call this mechanism *local error compensation*.

It was found that when an agonist finger was manipulated, the main mechanism of equilibrium maintenance was the local error compensation by the neighboring finger (Table 4). The distant error compensation was never used.

For the manipulation of the torque antagonists the results were mixed. These fingers exerted much smaller forces than the agonist fingers. Addition/removal of the L finger was not accompanied by statistically significant changes in other finger forces, whilst the addition/removal of the I finger was in part compensated by the changes in the force of the L finger (the distant error compensation).

In the non-zero torque tasks, the I addition and removal as well as L removal, were accompanied by the local error compensation, while during the L finger addition the distant error compensation was used (Table 5).

The changes in the tangential forces of the individual fingers after finger manipulation were diverse and did not follow a definite pattern that we would be able to sum up. We attribute this multiplicity to two factors: (1) redistribution of the total tangential force between the thumb and VF (for instance after the I finger addition the VF force decreases, see Table 2) – if a percentage contribution of a certain finger to the VF tangential force increases, this increase could be concealed by the VF force decline – and (2) during torque production, some finger force vectors in some performers (but not in all of them) are in the downward direction (see e.g. Zatsiorsky et al. 2003); averaging such data did not bring about statistically significant results.

DISCUSSION AND CONCLUSIONS

We will focus on discussing the three questions proposed at the beginning of this paper: (1) How is equilibrium maintained – do the thumb and virtual finger forces depend on a manipulated finger function or on the finger itself? (2) Does the behavior of the observed forces suggest feed-forward control? (3) Do the forces group into two subsets that support the principle of superposition? We also deliberate briefly on whether the principle of error compensation, which has been well established for multi-finger pressing tasks, is valid also for the studied prehension task.

How is equilibrium maintained?

The translational equilibrium in the horizontal and vertical direction was maintained by equal simultaneous changes of the thumb and VF force magnitudes in the same direction or opposite directions, respectively. The tilt prevention required more complex coordination.

During static grasping tasks the forces at the fingertips are arranged such that equilibrium is maintained. Removing or adding a finger requires redistributing the forces to maintain equilibrium. In the present study, during the non-zero torque tasks the normal forces changed according to the function of the finger – whether it was a torque agonist or antagonist (Table 1) – while the tangential forces changed according to the finger being manipulated (Table 2). In the former case there was a significant increase in grasping force when an agonist was removed or when an antagonist was added. In the zero-torque tasks, there was a significant increase of the grasping force when the I finger was added and when the L finger was removed; alternatively, a significant decrease was found when the L finger was added or the I finger was removed. These force adjustments represent a choice made by the central controller; they are not necessitated by the task mechanics.

When a finger was removed or added, the point of application of the VF normal force displaced. As a result, the changing moment of normal forces, M^n , perturbed rotational equilibrium of the handle (see equation 3, Methods). To maintain a constant moment on the handle and preserve the orientation, the central controller has the following options: (a) to adjust the normal forces among the fingers such that M^n remains at the pre-manipulation level, and/or (b) to produce a moment of tangential forces, M^t , such that it equilibrates M^n . If M^n does not change after a finger manipulation, this would mean that the effect of finger addition/removal was compensated by the redistribution of the normal forces among other fingers, i.e. option (a) is realized. Opposite changes of M^n and M^t indicate that the changes in M^n are compensated by M^t adjustments, i.e. option (b) is realized.

It is commonly accepted that control of prehension is organized in a hierarchical fashion and includes at least two functional levels: the VF level and the IF level (Arbib et al. 1985; Iberall, 1987; Santello, Soechting 2000; reviewed in Zatsiorsky, Latash 2008). Hence, the options described above can be reformulated as follows: is the error compensation and tilt prevention realized at the lower IF level (a), the higher VF level (b), or both (c)?

It seems that the answer should be (c), *both*. At the IF level the two strategies have been observed: (1) the *local error compensation*, i.e. enlisting a neighboring finger to compensate for the total force and moment disturbance, i.e. the M finger for the I finger manipulation and the R finger for the L finger manipulation, and (2) the *distant error compensation*, enlisting the L finger for the I finger manipulation and vice versa. The local finger compensation involves the force change opposite to the perturbation, i.e. force decrease/increase in response to the force increase/decrease; it compensates both for the VF force and moment changes. The distant error compensation aims at maintaining only the constant moment while exacerbating the VF force changes; in response to a finger addition/removal (force increase/decrease) the second finger changes the force magnitude in the same direction as the manipulated finger, thus enhancing the total force shift. While these strategies potentially can compensate for the M^n disturbances, they did this only in part. In a majority of the tasks—11 out of 12 (Table 3)—the M^n , and consequently the M^t , changed. Tilt prevention was achieved by the combined coordinated changes of the VF and thumb forces and the moments that they generate, i.e. it was achieved at the VF level of control hierarchy.

The chain effects—The data support the existence of the chain effects in the digit force adjustments to the finger addition or removal (the chain effects in multi-finger prehension are

reviewed in Zatsiorsky, Latash 2004 the chain effects in multi-finger prehension are reviewed in Zatsiorsky, Latash 2008), Figures 4 and 5.

The following chain of events can be traced in the figures: (a) finger addition/removal changes the moment of the normal forces exerted on the object → (b) the normal digit forces adjust to compensate for grip force which results in a change of moment of normal forces → (c) if there is a change in the moment of force due to the redistributed normal forces – which was observed in all cases except L removal during the PRO efforts – then the moment of tangential force changes to compensate → (d) the tangential VF and thumb forces change to produce the appropriate moment of tangential forces. The concurrent normal and tangential digit force adjustments can also be traced in the reverse order, specifically for the cases of the VF tangential force increase (a) or decrease (b). In case (a), the VF tangential force rise leads to an increase of a PRO moment (or decrease of a SUP moment); this upsurge is associated with the counter-moment of the normal forces in the SUP direction. In case (b), the decrease of the VF tangential force results in generating the moment in the SUP direction (or a decrease of the moment in the PRO direction); to prevent the object from tilting the latter moment is compensated by a counter-moment in the PRO direction by the normal forces. If there was no change in the tangential force, then no moment of force was created. On the whole, while the observed digit force changes look complex they all can be explained by the cause-effect chain of events.

On error compensation—The digit force adjustments to the finger manipulation can be viewed as an example of error compensation, an organizing principle of movement synergies (reviewed in Latash et al. 2007; Turvey 2007). In previous studies on error compensation in multi-finger tasks—tapping tasks (Latash et al. 1998) or pressing tasks (Li et al. 2003)—the performance variable that was kept relatively unchanged was the total force exerted by a group of fingers. In those studies, maintenance of the total force was not a mechanical requirement (no mechanical effects on the object were expected if the forces were not compensated), nor was it part of the instruction given to the subjects.

In the present study, only the local error compensation mechanism acted against the total force perturbations; the distant error compensation aggravated their effects on total force. So, what exactly is an ‘error’ in a complex hierarchical task involving many variables? Is the concept of ‘error’ applicable only to the performance variables at the top of control hierarchy or does it also extend to the lower hierarchical levels? It seems evident that during prehension any deviation from the handle equilibrium is an ‘error’ that has to be corrected (compensated). Equations (1)–(3) have to be satisfied and the resultant forces and moments acting on the object corrected if necessary. Yet, nothing in the equations tells why the VF normal force (if it equals the thumb force and is sufficiently large to prevent slipping) has to be corrected. If the above conditions are satisfied the VF force can be of any value. Hence, is the deviation of the grasping force from the pre-manipulation level an error that the central controller tries to correct?

Generally, if a simple task, e.g. exerting a force by several fingers, is included as a part in a more complex task, e.g. grasping an object and maintaining it at rest, is the synergy of the simple task completely aborted and replaced by another high-level synergy? Unfortunately, the present data do not provide a resolute answer to this question. However, the findings agree with recently published data on force stabilization in a two-hand force production task that involved two fingers per hand (Gorniak et al., 2007). The authors found significantly weaker, or even non-existent, two-finger force stabilizing synergies within-a-hand during two-hand tasks while such synergies were present in one-hand tasks. The authors have concluded that the CNS has limited ability to organize synergies at two levels of a control hierarchy simultaneously. There is an evident analogy with the findings of this study: perfect error compensation at the higher VF level and questionable error compensation at the lower IF level.

Are the digit force adjustments controlled in a feed-forward manner?—When a finger was being added or removed, the VF and thumb forces changed in synchrony (Figure 2) without a time delay with respect to each other (Figure 3). Also, in majority of cases, the force-force curves during the transition periods were either straight lines (Figure 3) or close to them. In other words, the changes of the thumb and VF forces were synchronous and perfectly coordinated. These data agree with an idea that the digit force adjustments during the object manipulation are controlled mainly in a feed-forward way. However, there were cases when the force-force relations showed signs of corrections and on-the-go adjustments, such as direction reversals. Hence, the feedback control can also be involved if necessary. Relatively large deviations of the moment magnitude from the nominal value during the transient periods suggest that the corrections were mainly necessary due to the tilting of the handle, while the object equilibrium in the horizontal and vertical directions was maintained with a higher precision. This is however only a supposition that requires future investigation.

Principle of superposition: The behavior of the tangential and normal forces may be due to the principle of superposition – there are two commands being sent to the system to maintain equilibrium: “grip harder or weaker” and “prevent tilting of the object.” In general the principle of superposition has been well documented (Zatsiorsky et al. 2004; Gao et al. 2006; Gao et al. 2005; Latash et al., 2004; Pataky et al. 2004b; Pataky et al. 2004a; Shim et al. 2005a; Shim et al. 2003a; Shim et al. 2005b; Zhang et al. 2006). Following the principle, the digit forces are organized into two subgroups with high correlation coefficients within the variables of one subgroup (close to ± 1.00) and low correlation coefficients (close to zero) with the variables from another group. It has already been mentioned that the changes in the moments of the tangential forces (Table 3) were in parallel with the changes in the forces themselves (Table 2), cf. ‘plus’, ‘equal’, and ‘minus’ signs in the cell of the above tables – they are the same. Nothing like that is seen when comparing Tables 1 and 3.

To demonstrate this assertion we plotted the data in two subplots (Figure 6, the left and right panels). For easier comparison with the published data, the figure is plotted in the form employed in previous publications (Zatsiorsky et al. 2004; Zatsiorsky and Latash 2004). The first group of variables included only two variables, the normal forces of the thumb and VF (Figure 6, upper left panel). The second group included the tangential forces of the thumb and VF and the moments of the normal and tangential forces (four panels on the right). The correlations (coefficients of determination) between the variables within each group were close to plus or minus one. As compared with these large correlations, the correlations between the variables from different groups, for instance between the VF normal force and the moment that this force generates were low (Figure 6, bottom left panel). The presented data agree well with the principle of superposition.

The data in the right part of Figure 6 may serve as an illustration of the chain effects explaining while the changes of the thumb *tangential* forces highly correlate with the moment of the *normal* forces. Starting from the upper left panel and moving clockwise the following relations can be observed: Panel I - F_{th}^t versus F_{vf}^t . The values of F_{th}^t and F_{vf}^t are on a straight line. This correlation was expected because $F_{th}^t + F_{vf}^t = \text{Constant}$ (weight of handle). The different location of F_{th}^t and F_{vf}^t values along the straight line signifies the different magnitude of M^t . Panel II - F_{vf}^t versus M^t [$M^t = 0.5(F_{vf}^t - F_{th}^t)d$, where $d = 73$ mm, see Figure 1]. As the sum F_{th}^t and F_{vf}^t is constant, a change in one of these forces determines the difference between their values and, hence, the moment that these force produce. Panel III - M^t versus M^n . As the sum of these two moments must stay constant, the contributing moments negatively correlate with each other. Panel IV - M^n versus F_{th}^t . The variables highly correlate with each other (‘without any evident reason’) due to the described chain effects. Not that the correlation of the F_{vf}^n with the M^n

(shown in panel B on the left) is very low. In other words, the correlation of the VF normal force with the moment that this force generates is low while the correlation of the tangential force with the moment is extremely large.

To summarize, the experiments have revealed two basic mechanisms of finger force adjustment, local and distant. The local mechanism seems to introduce minimal changes in the gripping force thus complying with the principle of error compensation. However, it requires higher absolute finger force changes because of the difference in the lever arms of the manipulated fingers (I and L) and their torque agonists (M and R). Furthermore, chain effects help understanding the sometimes non-trivial correlation patterns between pairs of elemental variables. The results support the principle of superposition.

References

1. Arbib, MA.; Iberall, T.; Lyons, D. Coordinated control programs for movements of the hand. In: Goodwin, AW.; Darian-Smith, I., editors. *Hand Function and the Neocortex*. Berlin: Springer Verlag; 1985. p. 111-129.
2. Arimoto S, Tahara K, Yamaguchi M, Nguyen PTA, Han HY. Principle of superposition for controlling pinch motions by means of robot fingers with soft tips. *Robotica* 2001;19:21–28.
3. Burstedt M, Flanagan J, Johansson R. Control of grasp stability in humans under various frictional conditions during multi-digit lifting. *Acta Physiol Scand* 1999;167:A22–A23. [PubMed: 10571582]
4. Flanagan, J.; Johansson, RS. Hand movements. In: Ramshandran, VS., editor. *Encyclopaedia of the human brain*. Academic Press; San Diego: 2002. p. 399-414.
5. Gao F, Latash ML, Zatsiorsky VM. Internal forces during object manipulation. *Exp Brain Res* 2005;165:69–83. [PubMed: 15912369]
6. Gao F, Latash ML, Zatsiorsky VM. Maintaining rotational equilibrium during object manipulation: linear behavior of a highly non-linear system. *Exp Brain Res* 2006;169:519–31. [PubMed: 16328302]
7. Gorniak SL, Zatsiorsky VM, Latash ML. Hierarchies of synergies: an example of two-hand, multi-finger tasks. *Exp Brain Res* 2007;179:167–8. [PubMed: 17103206]
8. Iberall, T. The nature of human prehension: Three dexterous hands in one. *Proc. 1987 IEEE Int. Conf. on Robotics and Automation*; Raleigh, NC. 1987.
9. Johansson RS, Westling G. Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. *Exp Brain Res* 1984;56:550–64. [PubMed: 6499981]
10. Kinoshita H, Kawai S, Ikuta K, Teraoka T. Individual finger forces acting on a grasped object during shaking actions. *Ergonomics* 1996;39:243–56. [PubMed: 8851529]
11. Latash M. There is no motor redundancy in human movements. There is motor abundance. *Motor Control* 2000;4:259–60. [PubMed: 10970151]
12. Latash ML, Li ZM, Zatsiorsky VM. A principle of error compensation studied within a task of force production by a redundant set of fingers. *Exp Brain Res* 1998;122:131–8. [PubMed: 9776511]
13. Latash ML, Scholz JP, Schoner G. Toward a new theory of motor synergies. *Motor Control* 2007;11(3):276–308. [PubMed: 17715460]
14. Latash ML, Shim JK, Gao F, Zatsiorsky VM. Rotational equilibrium during multi-digit pressing and prehension. *Motor Control* 2004;8:392–404. [PubMed: 15585896]
15. Li S, Latash ML, Zatsiorsky VM. Finger interaction during multi-finger tasks involving finger addition and removal. *Exp Brain Res* 2003;150:230–6. [PubMed: 12669172]
16. Pataky TC, Latash ML, Zatsiorsky VM. Prehension synergies during nonvertical grasping, I: experimental observations. *Biol Cybern* 2004a;91:148–58. [PubMed: 15378373]
17. Pataky TC, Latash ML, Zatsiorsky VM. Prehension synergies during nonvertical grasping, II: Modeling and optimization. *Biol Cybern* 2004b;91:231–4. [PubMed: 15503126]
18. Santello M, Soechting JF. Force synergies for multifingered grasping. *Exp Brain Res* 2000;133(4):457–67. [PubMed: 10985681]

19. Shim JK, Latash ML, Zatsiorsky VM. Prehension synergies: trial-to-trial variability and hierarchical organization of stable performance. *Exp Brain Res* 2003a;152:173–84. [PubMed: 12898101]
20. Shim JK, Latash ML, Zatsiorsky VM. The human central nervous system needs time to organize task-specific covariation of finger forces. *Neurosci Lett* 2003b;353:72–4. [PubMed: 14642441]
21. Shim JK, Latash ML, Zatsiorsky VM. Prehension synergies in three dimensions. *J Neurophysiol* 2005a;93:766–76. [PubMed: 15456799]
22. Shim JK, Latash ML, Zatsiorsky VM. Prehension synergies: trial-to-trial variability and principle of superposition during static prehension in three dimensions. *J Neurophysiol* 2005b;93:3649–58. [PubMed: 15728759]
23. Shim JK, Olafsdottir H, Zatsiorsky VM, Latash ML. The emergence and disappearance of multi-digit synergies during force-production tasks. *Exp Brain Res* 2005;164:260–70. [PubMed: 15770477]
24. Shinohara M, Li S, Kang N, Zatsiorsky VM, Latash ML. Effects of age and gender on finger coordination in MVC and submaximal force-matching tasks. *J Appl Physiol* 2003;94:259–70. [PubMed: 12391031]
25. Shinohara M, Scholz JP, Zatsiorsky VM, Latash ML. Finger interaction during accurate multi-finger force production tasks in young and elderly persons. *Exp Brain Res* 2004;156:282–92. [PubMed: 14985892]
26. Turvey MT. Action and perception at the level of synergies. *Hum Mov Sci* 2007;26:657–697. [PubMed: 17604860]
27. Zatsiorsky VM, Gao F, Latash ML. Finger force vectors in multi-finger prehension. *J Biomech* 2003;36:1745–9. [PubMed: 14522218]
28. Zatsiorsky VM, Latash ML. Prehension synergies. *Exerc Sport Sci Rev* 2004;32(2):75–80. [PubMed: 15064652]
29. Zatsiorsky VM, Latash ML, Gao F, Shim JK. The principle of superposition in human prehension. *Robotica* 2004;22:231–234.
30. Zatsiorsky VM, Latash ML. Multi-finger prehension: An overview. *Journal of Motor Behavior* (in press). 2008
31. Zhang W, Sainburg RL, Zatsiorsky VM, Latash ML. Hand dominance and multi-finger synergies. *Neurosci Lett* 2006;409:200–4. [PubMed: 17018249]

Figure 1.

Top panel: The handle with sensors and suspended load used during experimentation. Subjects used the bubble level on top of the apparatus to help maintain equilibrium. Bottom panel: Subject position during the experiment. Top view.

Figure 2. Changes in force vs. time plots during a trial with I addition, PRO effort (CW task), subject D: a representative example. The solid and dashed lines represent VF and thumb forces, respectively. The vertical line represents the time when the manipulated finger came into contact with the sensor. These signals have been subtracted by the average of the last one second prior to the manipulation

Upper panel: normal forces. The changes of the normal force magnitudes of the thumb and VF were both positive (increases) but for illustrative purposes they are plotted as plus/minus changes. These force-time histories were so similar that plotting them with the same sign, e.g. as force increases, resulted in two overlapping curves that were indistinguishable from each other. The grasping force (the algebraic sum of the VF and thumb normal forces) stayed constant.

Bottom panel: tangential forces. The changes were opposite and equal. The total tangential force does not change but the simultaneous increase/decrease of the thumb and VF tangential forces resulted in changing the load sharing between the VF and thumb.

Figure 3.
Exemplary plot of the thumb vs. VF normal force during a PRO effort and I finger removal task performed by a representative subject F ($r = 1.00$).

Figure 4.

Summary figure containing the average changes of the normal, tangential and the moments created for I and L addition, and each torque-task. A schematic.

Figure 5.

Summary figure containing the average changes of the normal, tangential and the moments created for I and L removal, and each torque-task. A schematic.

Figure 6.

The steady state values for the thumb and VF tangential force (F_{th}^t, F_{VF}^t), normal force (F_{th}^n, F_{VF}^n), tangential and normal moment components (M^t, M^n) **before** and **after** I finger removal. The black circles represent SUP efforts before finger removal and the grey squares represent SUP efforts after finger removal. Each marker represents an individual subject. The coefficient of determination (r^2) is labeled for each group within the figure.

Table 1

Changes in the thumb normal force during finger-addition and -removal tasks for (a) all non-zero torque tasks and (b) the zero torque tasks. The first numbers are group average (N). The p-values are in the parentheses. Standard errors across subjects are in italics. Plus/minus/equals signs designate the force increase, decrease or no significant change, respectively. CW/PRO - clockwise external torque, the subjects exert resisting moment in pronation; CCW/SUP - counterclockwise external torque, the subjects exert resisting moment in supination.

Manipulated finger	(a)			(b)		
	Finger addition, CW/PRO	Finger addition, 3-to-4 tasks CCW/SUP	Finger removal, 4-to-3 tasks CCW/SUP	Manipulated finger	Finger addition, 3-to-4 tasks	Finger removal, 4-to-3 tasks
Agonist	=1.56 (0.250) 1.23	=0.16 (0.811) 0.62	+2.31 (0.008) 0.60	I	+2.55 (0.030) 0.90	=-0.97(0.133) 0.56
Antagonist	+3.02 (0.028) 1.04	+2.77 (0.006) 0.67	-1.60 (0.011) 0.44	L	+2.24 (0.007) 0.55	=-0.88 (0.088) 0.44

Table 2
Changes in the tangential thumb force after (a) a finger was added and (b) a finger was removed. The same style is used as in the previous table (Table 1).

Manipulated finger	(a)			(b)		
	Finger addition, 3-to-4 tasks			Finger removal, 4-to-3 tasks		
	CW/PRO	ZERO	CCW/SUP	CW/PRO	ZERO	CCW/SUP
I	+2.88 (0.000) 0.27	+1.70 (0.000) 0.25	+0.70 (0.004) 0.16	-3.15 (0.001) 0.55	-1.67 (0.007) 0.42	-0.64 (0.019) 0.20
L	+0.29 (0.315) 0.27	-0.30 (0.002) 0.06	-0.87 (0.002) 0.17	+0.88 (0.001) 0.75	+0.96 (0.001) 0.16	+1.54 (0.001) 0.26

Changes in the moments of the tangential forces (Ncm) after (a) a finger was added and (b) a finger was removed. The same style is used as in the previous tables. The significance level $p=0.000$ corresponds to the cases where $p<0.001$. Cf. with Table 2.

Manipulated finger	a)			b)		
	Finger addition, 3-to-4 tasks			Finger removal, 4-to-3 tasks		
	CW/PRO	ZERO	CCW/SUP	CW/PRO	ZERO	CCW/SUP
I	-20.7 (0.000) 1.9	-12.3 (0.001) 1.8	-4.8 (0.007) 1.2	+22.4 (0.001) 3.8	+11.7 (0.007) 2.9	+4.2 (0.030) 1.5
L	=2.1 (0.367) 2.1	+2.2 (0.002) 0.4	+6.3 (0.002) 1.3	-6.1 (0.001) 1.1	-6.6 (0.001) 1.1	-11.5 (0.001) 1.9

Effects of manipulation of torque agonists: changes in finger normal force for non-zero torque conditions. The first number in the cells is the average change in force across subjects (newtons), the p-value is in the parentheses and the standard error is in italics. Manipulated fingers are in bold text. The data for the fingers that mainly compensated for the perturbation are underlined.

Finger Manipulation	Effect on the Normal Finger Force			
	I	M	R	L
Agonist Addition	I (PRO)	-4.1 (0.002) 0.76	=0.7 (0.146) 0.40	=0.1 (0.692) 0.23
	L (SUP)	-0.8 (0.050) 0.37	-2.1 (0.035) 0.76	+2.5 (0.003) 0.53
Agonist Removal	I (PRO)	-7.6 (0.000) 0.89	+2.6 (0.001) 0.38	+0.8 (0.007) 0.20
	L (SUP)	+0.5 (0.037) 0.18	+3.5 (0.000) 0.11	-3.0 (0.000) 0.40

Table 5
Changes in individual finger normal force during I and L addition and removal for the zero torque conditions. The data for the manipulated finger are in bold.

Finger Manipulation	Effect on the Normal Finger Force			
	I	M	R	L
I addition	+3.6 (0.000) 0.46	-1.2(0.003) 0.24	=0.1 (0.635) 0.23	=0.1 (0.504) 0.17
L addition	+1.0 (0.003) 0.27	=0.3 (0.174) 0.20	=0.1 (0.691) 0.23	+1.6 (0.000) 0.23
I removal	-3.2 (0.003) 0.65	+2.9 (0.002) 0.58	=0.8 (0.073) 0.37	=0.3(0.146) 0.21
L removal	=0.3 (0.158) 0.76	+0.7 (0.007) 0.17	+1.5 (0.005) 0.35	-1.6 (0.000) 0.22