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Multi-finger interaction during involuntary and voluntary single finger force changes

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Abstract

Two types of finger interaction are characterized by positive co-variation (*enslaving*) or negative co-variation (*error compensation*) of finger forces. Enslaving reflects mechanical and neural connections among fingers, while error compensation results from synergic control of fingers to stabilize their net output. Involuntary and voluntary force changes by a finger were used to explore these patterns. We hypothesized that synergic mechanisms will dominate during involuntary force changes, while enslaving will dominate during voluntary finger force changes. Subjects pressed with all four fingers to match a target force that was 10% of their maximum voluntary contraction (MVC). One of the fingers was unexpectedly raised 5.0 mm at a speed of 30.0 mm/s. During finger raising the subject was instructed “not to intervene voluntarily”. After the finger was passively lifted and a new steady-state achieved, subjects pressed down with the lifted finger, producing a pulse of force voluntarily. The data were analyzed in terms of finger forces and finger modes (hypothetical commands to fingers reflecting their intended involvement). The target finger showed an increase in force during both phases. In the involuntary phase, the target finger force changes ranged between $10.71 \pm 1.89\%$ MVC (I-finger) and $16.60 \pm 2.26\%$ MVC (L-finger). Generally, non-target fingers displayed a force decrease with a maximum amplitude of $-1.49 \pm 0.43\%$ MVC (L-finger). Thus, during the involuntary phase, error compensation was observed – non-lifted fingers showed a decrease in force (as well as in mode magnitude). During the voluntary phase, enslaving was observed – non-target fingers showed an increase in force and only minor changes in mode magnitude. The average change in force of non-target fingers ranged from $21.83 \pm 4.47\%$ MVC for R-finger (M-finger task) to $0.71 \pm 1.10\%$ MVC for L-finger (I-finger task). The average change in mode of non-target fingers was between $-7.34 \pm 19.27\%$ MVC for R-finger (L-finger task) and $7.10 \pm 1.38\%$ MVC for M-finger (I-finger task). We discuss a range of factors affecting force changes, from purely mechanical effects of finger passive lifting to neural synergic adjustments of commands to individual fingers. The data fit a recently suggested scheme that merges the equilibrium-point hypothesis (control with referent configurations) with the idea of hierarchical synergic control of multi-element systems.

Keywords

Synergy; hand; force; enslaving; equilibrium-point hypothesis

Introduction

It is well known that finger actions are interdependent. Two patterns finger interaction have been reported, positive co-variation (known as *enslaving*) and negative co-variation. During voluntary force production with a subset of fingers, the other fingers of the hand also

produce force in the same direction (*enslaving*, Zatsiorsky et al. 1998, 2000). Enslaving effect gets contribution from mechanical connections between the fingers (Fahrer 1981; Kilbreath and Gandevia 1994; Leijnse 1997), multi-digit motor units in the multi-tendon extrinsic muscles (Kilbreath and Gandevia 1994; Schieber 1995), and overlapping cortical representations of the intrinsic hand muscles (Schieber and Hibbard 1993; Sanes et al. 1995; Rathelot and Strick 2006).

A model was developed, the “mode hypothesis” (Danion et al. 2003, Zatsiorsky et al. 1998, 2002), which accounts for enslaving effects. This model was developed to study the neural mechanisms of finger coordination in multi-finger tasks. The hypothesis states that the neural controller manipulates hypothetical variables (modes) to individual fingers that reflect their intended involvement in the task. The mode magnitude represents an intensity of the central command intended for one finger but sent simultaneously to several fingers. Mode magnitude can vary from 0 to 1, with mode = 0 indicating zero intentional force production and mode = 1 representing maximal force production by a finger. For a more detailed discussion see Zatsiorsky et al. (2002). Analysis in terms of modes (rather than forces) allows, in particular, to address issues of task-specific co-variation of commands to fingers (reviewed in Latash et al. 2007).

The second type of finger interaction is characterized by negative co-variation (called in earlier studies *error compensation*, Latash et al. 1998) of finger forces, or force changes in opposite directions within a subset of fingers. Negative co-variation was found in multi-finger tasks in which subjects were asked to produce constant force with a set of fingers and then tapped with one of the fingers (Latash et al. 1998), added or removed a finger (Li S et al. 2003), increased the force of one finger voluntarily (Martin et al. 2009), or one finger was unexpectedly raised (Martin et al., in press). The negative co-variation of finger forces can be interpreted as resulting from a force-stabilizing synergy. This explanation follows from the definition of a motor synergy as a neural organization of elemental variables (in the present example, the finger forces) that stabilizes a performance variable (total force) by co-varied adjustments of the elemental variables (Gelfand and Latash 1998; reviewed by Latash et al. 2002, 2007).

The goal of this study has been to compare force changes in fingers of the hand when a finger force increases either (a) unintentionally, due to passive lifting; or (b) intentionally due to voluntarily pressing with a single finger.

Assuming that the subject is not voluntarily changing the modes to fingers when one finger is passively lifted, no effects of enslaving on other finger forces are expected. The force of the passively raised finger is expected to increase due to such factors as elastic properties of muscles (Magnusson 1998) and tendons (Benjamin et al. 2008), as well as the stretch reflex (Liddell and Sherrington 1924). In contrast, during intentional single-finger pressing, its mode is expected to increase, and enslaving is expected to lead to increased forces in all the fingers.

Negative co-variation is expected to reflect a pre-existent synergy associated with total force stabilization. A change in the force of the passively raised finger sensed by somatosensory receptors is an error signal, which is expected to lead to an unintentional decrease in all the other finger modes resulting in a drop in their forces. Hence, a task involving accurate, constant force production by a set of fingers is expected to be dominated by synergic mechanisms leading to negative co-variation (cf. Gorniak et al. 2007; Shapkova et al. 2008). So, we hypothesize that an involuntary increase in finger force will be associated with a drop in modes to other fingers and a drop in their forces. In contrast, a voluntary increase in

finger force is expected to lead to no changes in modes to other fingers; however an increase in forces will be observed due to enslaving.

We also explored two additional issues related to finger force adjustments. Previously, it was proposed that during multi-finger pressing the CNS attempts to minimize the 'secondary moment' produced about the longitudinal axis of the hand (Li ZM et al. 1998; Vigouroux et al. 2008). We hypothesized that a force changes of a finger, whether voluntary or not, will lead to force changes in other fingers that will be organized to minimize the moment about the longitudinal axis of the hand. The other issue is related to the effects of proximity on finger force adjustments, that is, whether fingers that are located closer to the task finger show larger mode/force adjustment as could be expected based on earlier studies (Zatsiorsky et al. 1998, 2000).

Methods and Materials

Subjects

Twelve subjects (six male, six female) participated in the experiment. The average age, weight, and height ($\pm$ SD) of the male subjects were 24.8 ± 3.2 years, 78.9 ± 4.8 kg, and 186.0 ± 4.8 cm, respectively. The average age, weight, and height of the female subjects were 23.0 ± 2.8 years, 62.6 ± 17.7 kg, and 162.1 ± 12.2 cm, respectively. All subjects were right-handed, in good health, and had no previous history of neuropathies or traumas to the upper limbs. None of the subjects were professional typists or musicians, which could affect finger coordination. The subjects gave informed consent according to the procedures approved by the Institutional Review Board of the Pennsylvania State University.

Apparatus (the 'inverse piano' technique)

The main piece of equipment was a device called the 'inverse piano' (I-Piano). The I-Piano consists of four uni-directional piezoelectric force transducers (208C02, PCB Piezotronics) mounted on top of four linear actuators (PS01-23 $\times$ 80, Linmot, Spreitenbach, Switzerland) (Figure 1). Actuators produced smooth vertical movements of the transducers. The I-Piano was mounted to a steel frame that was rigidly attached to the testing station. Each individual transducer/actuator combination was adjustable in the finger longitudinal direction, but not in the medial/lateral direction. Actuators were adjusted prior to each subject's testing session in a configuration they reported as being most comfortable, which was typically exemplified by approximately 0 degrees of flexion at MCP joint, 30–45 degrees flexion at PIP joint, and 30–45 degrees of flexion at DIP joint. A wooden block was placed in the palm of the hand to support the hand and limit wrist flexion as well as supination/pronation of the forearm. The block provided support to the hand across the 2–5 metacarpal bones. The thumb was abducted and flexed so that it was against the side of the wooden block and supported in the vertical direction by a wooden platform. The wooden platform extended towards the subject and provided support to the entire forearm, from wrist to elbow.

The transducers were calibrated prior to data collection in the first subject. Sandpaper pads were attached to the contact surface of the force transducers to increase friction and to reduce the temperature effect from the skin. Analog output signals from the transducers were connected to separate AC/DC conditioners (484B, PCB Piezotronics, Depew, NY, USA), then digitized using a 16-bit analog-digital converter (CA-1000, National Instruments, Austin, TX, USA), mounted on a microcomputer (Dimension 2400, Dell, Round Rock, TX, USA) that was utilized for control, acquisition, and processing of the data. The actuators were programmed using LabVIEW (LabVIEW Version 8.0, National Instruments) that sent commands to a controller (E400-AT, Linmot, Spreitenbach, Switzerland).

Experimental Procedure

The experiment consisted of three separate measurement sessions. During all sessions, subjects were seated facing the testing table with the right upper arm at approximately 45° shoulder abduction in the frontal plane, 45° shoulder flexion in the sagittal plane, and approximately 45° flexion of the elbow. The first session was used to measure individual finger maximum voluntary contractions (MVC). MVC measurements were recorded for each finger individually and all four fingers together in five different hand configurations. The hand configurations were all fingers level (C_0), I-lifted (C_I), M-lifted (C_M), R-lifted (C_R), and L-lifted (C_L). Measurements were made for the different hand configurations because the changes in muscle architecture would affect the force producing capabilities of the fingers. The height of the key for the passive finger lift was 5.0 mm. MVC trials were 5 s long during which subjects were instructed to press with a given finger to achieve maximal force and maintain it for approximately 1 s (Figure 2a). The peak force was taken as the MVC value. There were 25 MVC trials (5 MVC measurements $\times$ 5 hand configurations = 25).

During the second session subjects had to follow a ramp target force with each finger for all of the hand configurations (Figure 2b). The ramp started at 0% MVC and went up to 70% MVC at a slope of 10% MVC/s, thus trials were 7 s in duration. The MVC force levels were based on the MVC values recorded for each hand configuration in the first session. The force data of all four fingers were recorded during each trial. There were 20 ramp trials performed (4 fingers $\times$ 5 hand configurations = 20 trials).

The third session was the main experimental session. Subjects were given a force target range to which they were instructed to press with all four fingers and keep the force inside the target range. The feedback was the total force produced by all four fingers. The target range was of 10% MVC $\pm$ 5.0% of four-finger pressing in hand configuration C_0 . Once the force output initially reached the target range it had to remain within the target range prior to the initial perturbation, otherwise the trial was aborted and restarted. After 5 s one of the transducers was lifted to 5.0 mm at 3.0 cm/s. Subjects were told one of the keys would be lifted and, when this occurred, “do not intervene voluntarily”. One second prior to the key being lifted, the actual force feedback was removed and replaced with pseudo-feedback for the remainder of the trial. The pseudo-feedback was a sinusoidal signal with noise added that always remained within the force target range. This pseudo-feedback was used so that subjects were not surprised by the sudden change in force from key being lifted and attempt to actively change their finger force to match the target force. After the key was lifted, the next instruction was to wait for about 3 s, and then quickly press down with the lifted finger only to produce a pulse of force. The subjects were told to press with as close to maximal effort as they could *without* a change in arm posture or fingers losing contact with force sensors. Many of the male subjects were able to press the sensor with a force greater than that being produced by the linear actuator, which caused it to lower back to its initial position. If subjects demonstrated this ability then they were told to attempt to press the motor down to the initial position every time. In terms of pulse speed and duration they were told to produce the force pulse as quick as possible then immediately return back to the target force. The experimenter showed subjects examples of what a desired force pulse profile appeared like.

A short practice session was performed until subjects demonstrated that they were able to follow these instructions. The actual force feedback of the trial was visible to the experimenter and it was quite apparent if the subject followed the instructions. There were 20 total trials (4 fingers $\times$ 5 trials per finger = 20 trials). The passive finger lifting phase of the experiment will be referred to as the involuntary phase (*Invol*) and the finger pressing phase will be referred to as the voluntary phase (*Vol*). The finger that was passively lifted

and then pressed voluntarily will be referred to as the target finger and the other fingers referred to as non-target fingers.

Data Processing

A custom LabVIEW program (LabVIEW Version 8.0, National Instruments) was used to collect the force signals and display feedback to subjects. The actuator moves were controlled within the program. This allowed for the exact time of actuator move initiation to be known. Force data were collected at a frequency of 300 Hz. The force data were filtered using a 4th order low-pass two-way Butterworth filter at 10 Hz using Matlab (Version R2006a, The Mathworks, Inc). All trials were inspected to verify that subjects followed the instructions. The criteria for an acceptable trial was: (1) once the total force was within the target range it remained in the range until the actuator move was initiated, (2) the sharing pattern was steady during the first 5 s, (3) the target finger displayed an increase in force during the upward move of the actuator, and (4) a quick force pulse was produced with a force profile that was qualitatively similar to what the instruction was.

Data Analysis

The data of interest were the changes in both actual forces (**F**) and mode (**MD**) values expressed in newtons during passive finger lifting and pressing. The method of computing **MD** values is described below. The force and mode changes (ΔF and ΔMD) during key lifting were computed as the difference between the values at the time of peak force of the lifted finger minus the average value over 250 ms prior to initiation of key upward movement. To find the onset of the *Vol* phase, the rate of force change (dF/dt) was calculated for the target finger over the *Vol* phase of the trial. The maximum dF/dt was identified and the initiation of *Vol* pressing was assumed to occur when dF/dt reached 5% of this value. Trials were inspected visually to ensure that the identified time of initiation of finger pressing and peak force was correct.

The **F** data were transformed to **MD** values. The first step was to construct the enslaving matrix, which was calculated from the ramp-target trials. For each ramp-target trial, linear regression coefficients were computed on the force of each finger against the total force of all four fingers from 0% to 50% MVC range of the instructed finger. The coefficient of the regression line for each finger was entered into the enslaving matrix:

$$Enslaving\ Matrix = \begin{bmatrix} b_{i,i} & b_{i,m} & b_{i,r} & b_{i,l} \\ b_{m,i} & b_{m,m} & b_{m,r} & b_{m,l} \\ b_{r,i} & b_{r,m} & b_{r,r} & b_{r,l} \\ b_{l,i} & b_{l,m} & b_{l,r} & b_{l,l} \end{bmatrix} \quad (1)$$

where $b_{j,k}$ is the regression coefficient of individual finger F_j [$j = \{\text{index}(i), \text{middle}(m), \text{ring}(r), \text{little}(l)\}$] when finger k is instructed to press [$k = \{\text{index}(i), \text{middle}(m), \text{ring}(r), \text{little}(l)\}$]. Separate enslaving matrices were computed for each of the five finger configurations (C_0 , C_I , C_M , C_R , and C_L). The mode value in newtons, **MD** was computed by multiplying the inverse of the appropriate enslaving matrix (for a given finger configuration) by the recorded **F** values:

$$MD = E^{-1} * \begin{bmatrix} F_i \\ F_m \\ F_r \\ F_l \end{bmatrix} \quad (2)$$

The C_0 finger configuration enslaving matrix was used to calculate the **MD** values during key lifting. **MD** values during the *Vol* pressing phase were computed using the appropriate raised finger enslaving matrix (finger configuration C_I , C_M , C_R , and C_L). The ΔMD of each finger during passive finger lifting and voluntary pressing was calculated in the same manner as described for ΔF .

Due to gender strength differences, there was a large variation in the magnitude of ΔF across subjects. In order to compare ΔF and ΔMD values across subjects they were normalized to the MVC values of the respected finger. During each phase of the experiment, the ΔF and ΔMD of both the target finger and non-target fingers were compared.

An index, called the compensation percentage (COMP%), was calculated to quantify the synergic relationship between the fingers during the *Invol* phase. It was assumed that a force-stabilizing synergy among the fingers was established during the steady-state phase of each trial. The COMP% quantifies the strength of the synergy in terms of how much of the ΔF of the lifted finger is compensated for by ΔF of the non-lifted fingers, with 100% indicating that the overall effect of total force was nil. The COMP% is computed as:

$$100*[1 - (\sum_j \Delta F_j)/\Delta F_{\text{raised}}] \quad (3)$$

where F_j is the set of individual finger ΔF [$j = \{\text{index (i), middle (m), ring (r), little (l)}\}$].

The change in moment about the longitudinal axis of the hand during *Invol* and *Vol* was another parameter of interest. The moments produced by the target finger force and all finger forces together about the neutral line (NL) were compared. The NL was the point of application of the resultant normal force by all fingers in the medial-lateral direction. The location of the neutral point of normal F application of the fingers was found using the following formula (Zatsiorsky et al. 1998):

$$NL = \frac{\sum_j F_j * L_j}{F_{\text{tot}}} \quad (4)$$

where NL is the medial-lateral coordinate of the neutral point of normal force application, F_j [$j = \{\text{index (i), middle (m), ring (r), little (l)}\}$] is the finger normal force, L_j is the moment arm of each finger, and F_{tot} is the sum of the normal forces of all fingers. The moment arms (L_j) of the individual finger forces were measured from the index finger with $L_i = 0$ mm, $L_m = 30$ mm, $L_r = 60$ mm, and $L_l = 90$ mm. After the perturbation (*Invol* or *Vol*) the change in the moment about the NL was computed in regards to: (1) ΔF and ΔMD of the target finger only ($MD_j = (L_j - NL) * f_j$), and (2) ΔF and ΔMD of all fingers ($M_{\text{TOT}} = \sum [(L_j - NL) * f_j]$).

The effect of proximity of non-target fingers to target finger was investigated. Fingers were assigned a proximity value of 1, 2, or 3 in terms of the distance from the target finger, where the finger(s) adjacent to the target finger was assigned a value of 1. When either the M- or R-fingers were the target finger there were two adjacent fingers.

Statistical Analysis

Mean and standard errors (SE) of the ΔF , ΔMD , proximity index changes, change in moments about NL, were computed across all subject trials of the same condition. Paired t-tests were used to test for a significant difference between various measures between: (1) ΔF and ΔMD values in the same phase of a trial (*Invol* or *Vol*) and (2) between *Invol* and *Vol* phases of a trial. One-way repeated measures ANOVAs were used to test for the effect of

Finger perturbed (4 levels: I, M, R, and L) on the *Invol* and *Vol* responses of: *Target Finger* ΔF and ΔMD , *Non-Target Finger* ΔF and ΔMD , *Total* ΔF and ΔMD . One-way repeated measures ANOVAs were used to test for the effect of *Proximity* (3 levels: 1, 2, and 3) on the ΔF and ΔMD in un-perturbed fingers. Tukey pairwise comparisons were performed to test the difference among levels of each ANOVA test. Statistical analysis was performed using the statistical software Minitab 13.0 (Minitab, Inc., State College, PA, USA) and SPSS (SPSS Inc., Chicago, IL, USA). The data were tested for sphericity and deviations were corrected using the Greenhouse-Geisser correction. All statistical analysis was performed at a significance level of $\alpha = 0.05$.

Results

Changes in forces and modes during the involuntary phase

The force changes (ΔF) and mode changes (ΔMD) values averaged across subjects during the involuntary phase (*Invol*) are illustrated in Figure 3.

Changes in forces—In all cases, the average ΔF of target fingers was positive and in all but one case the average ΔF of non-target fingers was negative, i.e. negative co-variation, not enslaving was observed. The target finger displayed a ΔF between $10.71 \pm 1.89\%$ MVC (I-finger) and $16.60 \pm 2.26\%$ MVC (L-finger). For all subjects the total force (i.e. force produced by all fingers) increased. The percentage of ΔF of the target finger compensated for by the negative ΔF of the non-target fingers was computed (COMP%). The COMP% by the non-raised fingers ranged from $17.0 \pm 9.0\%$ MVC (L-finger raised) to $24.9 \pm 6.4\%$ MVC (R-finger raised), i.e. the compensation was present but not complete ($\Delta F_{\text{total}} > 0$). The one-way repeated measure ANOVAs (Table 1A) showed that the effect of *Finger* perturbed was significant on the ΔF of the target finger, non-target fingers, and total force. The effect of *Proximity* of non-target fingers to the target finger was examined. The *Proximity* effect on the ΔF of non-target fingers was significant ($p < 0.001$). Fingers with a closer proximity to the target finger had a larger decrease in force during the passive lifting of the target finger. The averaged ΔF data, as a function of proximity to target finger, is presented in Figure 4. Pairwise comparisons showed that the ΔF for a proximity of 1 was significantly different than the ΔF for a proximity of 3 ($p < 0.01$) and a proximity of 2 was significantly different than a proximity of 3 ($p < 0.01$).

Changes in mode magnitudes—Mode changes (ΔMD) of target fingers ranged from $12.05 \pm 1.90\%$ MVC (I-finger) to $29.06 \pm 3.19\%$ MVC (L-finger). In all cases the ΔMD of non-target fingers was negative. The largest ΔMD of a non-target finger was $-6.24 \pm 1.24\%$ MVC (L-finger when R-finger raised). The total ΔMD (sum of ΔMD of individual fingers) was positive for all trials. The COMP% by the non-target fingers ranged from $26.6 \pm 9.0\%$ MVC (I-finger raised) to $50.6 \pm 7.1\%$ MVC (R-finger raised). ΔMD values of *Target Finger*, *Non-Target Finger*, and *Total* ΔMD were all significantly affected by *Finger* raised (Table 1B). A significant *Proximity* effect was found ($p < 0.001$), with fingers closer to the target finger displaying a larger negative ΔMD . Pairwise comparisons found that the ΔMD with a proximity of 1 was significantly different than the ΔMD for a proximity of 2 or 3 ($p < 0.001$).

Comparison of force and mode changes—The ΔF and ΔMD were compared for both target and non-target fingers. The ΔF and ΔMD of the target fingers were significantly different for all fingers (Figure 4), with the ΔMD of the target finger being larger than the ΔF . The ΔF and ΔMD of the non-target fingers were significantly different in 6 of 9 instances. In general, the ΔMD was larger in magnitude than ΔF for the non-target fingers.

Changes in forces and modes during the voluntary phase

The force changes (ΔF) and mode changes (ΔMD) values averaged across subjects during the voluntary phase (*Vol*) are shown in Figure 5.

Changes in forces—The target finger showed a large positive ΔF , between $90.61 \pm 13.65\%$ MVC (R-finger) and $64.61 \pm 6.60\%$ MVC (I-finger). All non-target fingers displayed a positive ΔF , which was larger for fingers adjacent (proximity = 1) to the target finger (proximity effect). The average positive ΔF of non-target fingers ranged from $21.83 \pm 4.47\%$ MVC for R-finger (M-finger instructed to press) to $0.71 \pm 1.10\%$ MVC for L-finger (I-finger instructed to press). One-way ANOVA showed a significant effect of *Finger* on the ΔF of the *Target Finger*, *Non-Target Fingers*, and *Total ΔF* (Table 1B). A significant *Proximity* effect was found for ΔF of non-target fingers. Fingers with a closer proximity to the target finger showed larger increase in force during the pressing of the target finger. Pairwise comparisons found that the ΔF of non-target fingers with a proximity of 1 was significantly different than the ΔF for proximities of 2 and 3 ($p < 0.001$).

Changes in modes—The average ΔMD of the target fingers were between $140.57 \pm 25.75\%$ MVC (R-finger) and $68.55 \pm 6.69\%$ MVC (I-finger). In 7 of 12 cases a negative ΔMD was observed for the non-target fingers. The range of ΔMD for non-target fingers was between $-7.34 \pm 19.27\%$ MVC for R-finger (L-finger instructed to press) and $7.10 \pm 1.38\%$ MVC for M-finger (I-finger instructed to press). In terms of ΔMD values, the *Finger* effect was significant on the change in *Target Finger* and *Total ΔMD* . There was no significant effect of *Proximity* on non-target finger ΔMD ($p > 0.35$).

Comparison of force and mode changes—The ΔF and ΔMD of the target fingers were found to be statistically significantly different for R- and L-fingers (Figure 5). On average the ΔMD was larger than the ΔF for all the target fingers. The ΔF and ΔMD of the non-target fingers were significantly different in 5 of 9 instances. In general the ΔMD was smaller in magnitude than the ΔF for the non-target fingers. In many of the cases the ΔMD was very close to zero.

Secondary Moment Stabilization

The moment produced about the NL by target finger ΔF and ΔF of all fingers together (target finger and non-target fingers combined) were significantly different for both phases (*Invol* and *Vol*) (p -value < 0.001). The same was found in regards to ΔMD values. In regards to the *Invol* phase, the total moment change was *larger* when M-, R- and L- fingers were raised than the moment change produced by the target finger alone. This indicated that the force changes, both ΔF and ΔMD in the non-target fingers *did not* act to compensate for the moment change due to the target finger perturbation. The opposite was found for *Vol*. For all *Vol* target finger trials the total moment was *smaller* than the moment produced by the target finger alone (Table 2). This was true when the moment change was computed in regards to both F and MD values. This indicated that the force changes in the non-target fingers functioned to *compensate* for the moment change produced by the target finger force increase.

Discussion

The results agree well with the main hypotheses. In particular, the first hypothesis was that during the involuntary finger force increase (*Invol* phase) finger force adjustments will primarily reflect a force stabilizing synergy. The data support this hypothesis: For all conditions the target finger displayed an increase in force and the non-target fingers showed a decrease in force. This finding was upheld when the analysis was performed in terms of

both force (F) and mode (MD) values. The compensation of the force increase in the target finger by the force drop in the non-target fingers was far from complete, between 20 and 25%.

A previous study (Martin et al. 2010, *in press*) showed qualitatively similar results during involuntary force changes. It was found that initial pressing force had a highly significant effect on the force changes observed during passively lifting one of the fingers. It is possible that the low initial pressing force used in this experiment did not allow stronger effects of the force-stabilizing synergy to emerge. Higher compensation values were reported by Latash et al. (1998). In that study subjects were asked to tap with one finger after initially pressing with I-, M-, and R-fingers to 30% MVC. Compensation by non-tapping fingers for the tapping finger force drop to zero was, on average, between 94% and 102%.

The second hypothesis was that, during the voluntary force production by the target finger, the force of the non-target fingers would increase without a change in modes to those fingers that is exclusively due to enslaving. During the *Vol* phase all of the non-target fingers showed substantial increases in force but only very small changes in mode values. This signifies that, when instructed to press with a target finger, subjects were able to direct the command (the mode) almost entirely to the target finger with force changes in the other fingers produced by the enslaving. The changes in the non-target finger forces displayed a strong proximity effect similar to that documented in previous enslaving studies (Zatsiorsky et al. 1998; 2000). However, the changes in the mode values showed no proximity effect, which supports the conclusion that subjects were able to send the pressing command solely to the target finger.

The third hypothesis was that during both phases the force changes of non-target fingers would act to reduce the moment about the longitudinal axis of the hand. The data do not allow support the claim that the synergic reactions during the *Invol* phase acted to minimize the secondary moment. However, during the *Vol* phase this hypothesis was upheld. When analyzed in terms of both forces and modes, the total moment change was smaller than the moment change induced by the target finger alone. This was true for all target fingers. A similar finding was reported by Vigouroux et al. (2008); however, they used a four-finger pressing task instead of single-finger pressing used in our experiment.

Factors Contributing to Force Changes

Several mechanisms could lead to force changes. The first, most basic, mechanism is purely mechanical. There are mechanical effects of passively lifting a finger that can cause changes in the forces of other fingers. A study (Martin et al. 2010) that was performed prior to this study investigated force changes during the *Invol* phase. Several levels of initial pressing force, vertical displacement and vertical speed were used. To ensure that the force changes were not purely passive a force changes were recorded while subjects passively rested their non-raised fingers were smaller than during active finger pressing, even positive in some cases. The conclusion was that the force changes during the experimental trials could not be explained solely by the passive mechanics of finger lifting. Besides the immediate effects of lifting mechanics forces can be transmitted between fingers due to deformation of tissues connecting the fingers. These would be expected to be more prominent in the *Vol* phase than *Invol* due to higher forces, and thus higher internal strains. It is almost certain that mechanics do contribute to the force changes; however, they are evidently not the sole cause. Another method to assess whether or not force-changes are due to mechanical effects is to measure the latency between the lifted finger and non-lifted finger force changes. This works well for some experimental tasks; however, for this particular study we did not deem it appropriate. The force changes of the non-lifted fingers were quite small and it was difficult to define when they started to deviate from the background force. Based entirely on

visual inspection the force changes of non-lifted fingers did appear to have a greater than zero-latency, which supports the contention that force changes were due to more than pure mechanical effects.

Another potential cause of the force changes are reflex responses. Changes in muscle length induce the stretch reflex (Liddell and Sherrington 1924; Matthews 1959). However, given the small amplitude of finger raise and the low speed of this motion, the reflex effects were likely modest (Matthews 1959; Rack and Westbury 1969). Also, the stretch reflex evoked during the *Invol* phase in the extrinsic flexors would produce a force increase in all non-task fingers, not a force decrease as observed in the experiments.

A third mechanism of the observed force changes is enslaving. As already mentioned enslaving can be due to mechanical connections between the fingers (Fahrer 1981; Kilbreath and Gandevia 1994; Leijnse 1997), multi-digit motor units of the extrinsic muscles (Kilbreath and Gandevia 1994; Schieber 1995), and overlapping cortical connections (Schieber and Hibbard 1993; Sanes et al. 1995; Rathelot and Strick 2006). The enslaving effects were assumed to be present in both the *Invol* and *Vol* phases. They were expected to dominate in the *Vol* phase and might have been masked in the *Invol* phase by the more dominant total force-stabilizing synergic relationship that was established prior to the finger lifting.

A total force-stabilizing synergy is the last mechanism of force changes in the fingers that we will be considering. We use a definition of a synergy as a neural organization of elemental variables in a way that reduces the variability of an important performance variable (reviewed in Latash et al. 2007; Latash 2008). For a multi-finger pressing task, in which the instruction was to produce a certain level of force, the elemental variables would be each finger's force or mode while the performance variable is the total force. Negative force changes displayed by the non-target fingers in response to the positive force change of the target finger during the *Invol* phase may be seen as signs of such a synergy. Several recent studies provide support to the possibility that a total force stabilizing synergy commonly exists among the fingers during multi-finger pressing (Gorniak et al. 2007; Shapkova et al. 2008).

Aside from the above mentioned factors that could cause force changes there are other factors that affect the magnitude of the force changes by altering motor unit recruitment thresholds. McNulty and Cresswell (2004) studied the effect of varying muscle length and load on the recruitment behavior of low threshold motor units in the flexor digitorum superficialis. They found that at shorter muscle lengths the recruitment threshold was decreased with increased loads. At longer muscle lengths the recruitment threshold was less affected by external load, equivalent to initial pressing force in our study. These factors should be taken into consideration when interpreting the results of this study.

Perhaps the main limitation of this study was that our protocol did not allow the individual mechanisms (i.e. mechanical, neural, etc.) of force changes to be estimated. As previously stated, finger interaction is a complex combination of mechanical and neural factors. Recently, several studies have used EMG in an attempt to estimate the force distribution of extrinsic forearm muscle motor units across the fingers (Keen et al. 2004; Butler et al. 2005). Butler et al. (2005) recorded EMG from individual motor units of the flexor digitorum superficialis during flexion at various contraction levels. The results showed that below 50% MVC the recruitment of motor units serving individual digits was quite independent. Keen et al. (2004) performed a similar experiment involving the extensor digitorum. The main finding was that the force output of single digits from microstimulation of single motor units of the extensor digitorum was also quite concentrated to individual

digits. These studies point toward the conclusion that, at least in terms of the neural enslaving factors, fingers are more independent during low level force production. This suggests that at low force production levels the forces produced by fingers are very close to the intended force production of the central nervous system, minus the enslaving that occurs due to mechanical factors. This would allow for fine object manipulation, which commonly utilizes relatively low force production.

Negative vs. Positive Force Co-variation

The two basic patterns of finger interaction were clearly exemplified during the *Invol* and *Vol* phases of the experiment. The *Invol* phase was characterized by a negative co-variation of finger forces (error compensation, Latash et al. 1998). Error compensation is a fundamental feature of motor synergies and, as previously demonstrated, transcends tasks in which the performance variable (such as total force) is the same but perturbations differ (tapping, finger addition/removal, passive finger lifting, Latash et al. 1998; Li S. et al 2003; Martin et al. 2009, 2010).

The *Vol* perturbation was a clear example of finger enslaving (Zatsiorsky et al. 1998; 2000). Similar to previous studies, the task was to produce force with a single finger; however, other fingers also showed substantial increases in their force production. The force production of the non-target, or enslaved fingers, displayed the same fundamental characteristics as previously documented: 1) relatively large force changes that ranged from $21.83 \pm 4.47\%$ MVC (R-finger, M-pressing) to $0.71 \pm 1.10\%$ MVC (L-finger, I-pressing); 2) proximity effect in which the adjacent (proximity = 1) fingers to the target finger produced the largest forces; and 3) a higher independence, or less enslaving, of the I-finger compared to other fingers. The changes in the mode values of non-target fingers during the *Vol* phase were, on average, very close to zero. This indicates that the amount of enslaving during rapid finger pressing differed very little from the enslaving trials that were performed to compute the enslaving matrices.

The common connection, in terms of control, between error compensation and enslaving is that both have a strong neural origin. The fact that the subjects essentially switched from one pattern to another within a single short trial suggests that the CNS is capable of regulating which pattern emerges with relative ease and that the mechanical connections between the fingers play less of a role in the finger force interaction than the neural component. Further evidence supporting the notion that finger interaction depends more on neural mechanisms than the architecture of the periphery is that obviously the connections between the fingers didn't change between *Invol* and *Vol* phases yet different interaction patterns emerged. Perhaps, the next step in this line of research is to design experimental protocols that can identify the relative contribution of each mechanism to the observed force changes.

Interpretation within the Equilibrium-Point Hypothesis

The equilibrium-point hypothesis (Feldman 1966, 1986) was originally developed for single-muscle control; it assumes that the voluntary command to a muscle can be adequately described as changes in the threshold of the tonic stretch reflex. Later, the hypothesis was developed for multi-muscle systems and whole-body movements in the form of the referent configuration hypothesis (Feldman, Levin 1995). Recently, the main ideas of the referent configuration hypothesis have been merged with the ideas of synergic control of multi-element systems (Latash 2010a,b; Latash et al. 2010). This approach considers a multi-level hierarchical control system where, at each level, control variables represent levels of subthreshold depolarization of neuronal pools that, in their interaction with the external force field, specify referent coordinates of important performance variables. The difference between the referent and actual coordinates of a variable drives muscle activation directed at

moving the actual coordinate towards the referent one. If an external obstacle prevents movement, active force generation is observed at equilibria.

When the subject was asked to produce a certain value of the total force, a referent coordinate of a “virtual finger” (an imaginary digit with the mechanical effect equal to that of all the actual fingers combined, Arbib et al. 1985) was established at the highest, task level of the hierarchy. This coordinate served as an input into a synergic organization that produced referent coordinates for individual fingers that differed in different trials as long as the effects of this variability on the referent coordinate of the virtual finger were small. This is reflected in negative across trials co-variation of finger forces (and modes) stabilizing the total force value (see Latash et al. 2001; Gorniak et al. 2007; Shapkova et al. 2008). When a finger was passively lifted, the instruction “not to interfere” implied no changes in the referent coordinate of the virtual finger. The mentioned synergic mechanism, however, used somatosensory information on the target finger force increase to drive adjustments of referent coordinates to non-target fingers. These adjustments resulted in reproducible changes in the non-target finger modes. Since the point of virtual finger force application shifted away from the referent coordinate, there was an increase in the total finger force (that is, negative co-variation produced only partial compensation of the target finger force change).

During the *Vol* phase, when one finger was instructed to produce force, the task was effectively split into two: The target finger was controlled at the highest hierarchical level. Besides, the total force of the three non-target fingers was expected to remain unchanged. As a result, there was no synergic interference between the target and non-target fingers resulting in no adjustments in non-target finger referent coordinates (and no mode changes).

Another finding that allows interpretation within this theoretical scheme is the minimization of secondary moments supported by the findings on the neutral line (NL) coordinate changes. Referent configuration does not have to be limited to a single variable such as, for example, total force which was used to set tasks in our study. In particular, a set of referent values for several performance variables may be set at the highest, task-related, hierarchical level. One of such variables may be coordinate of the NL in the medio-lateral direction (supported by Latash et al. 2001; Scholz et al. 2002). Note that several recent studies have shown that multi-digit synergies are able to stabilize several variables at the same time, even if explicit feedback and task formulation focused on only one of those variables (Zhang et al. 2008; Klous et al. 2010) indirectly supporting our interpretation.

Overall, the results of this study fit well the framework of the equilibrium-point hypothesis coupled with the idea of multi-finger synergies.

Although we used a rather artificial task and experimental design to study finger interaction, the findings have direct implications for finger interaction during many common situations encountered when manipulating objects. The involuntary phase may be compared to a situation when a person is holding an object and it suddenly deforms, for example as during holding a plastic cup filled with water. The voluntary phase may be compared to holding an object and then changing finger location, lifting a finger or re-positioning it on the object.

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References

- 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.
- Benjamin M, Kaiser E, Milz S. Structure-function relationships in tendons: a review. *J Anatomy*. 2008; 212:211–228.
- Butler TJ, Kilbreath SL, Gorman RB, Gandevia SC. Selective recruitment of single motor units in human flexor digitorum superficialis muscle during flexion of individual fingers. *J Physiol*. 2005;301–309. [PubMed: 15946972]
- Danion F, Schoner G, Latash ML, Li S, Scholz JP, Zatsiorsky VM. A mode hypothesis for finger interaction during multi-finger force-production tasks. *Biol Cybern*. 2003; 88:91–98. [PubMed: 12567224]
- Fahrer, M. Interdependent and independent actions of the fingers. In: Tubiana, R., editor. *The hand*. Philadelphia: Saunders; 1981.
- Feldman AG. Functional tuning of the nervous system with control of movement or maintenance of a steady posture. II. Controllable parameters of the muscle. *Biophysics*. 1966; 11:565–578.
- Feldman AG. Once more on the equilibrium-point hypothesis (λ -model) for motor control. *J Mot Behav*. 1986; 18:17–54. [PubMed: 15136283]
- Feldman AG, Levin MF. Positional frames of reference in motor control: their origin and use. *Behav Brain Sci*. 1995; 18:723–806.
- Gelfand IM, Latash ML. On the problem of adequate language in motor control. *Motor Control*. 1998; 2:306–313. [PubMed: 9758883]
- Gorniak S, Zatsiorsky VM, Latash ML. Hierarchies of synergies: An example of the two-hand, multi-finger tasks. *Exp Brain Res*. 2007; 179:167–180. [PubMed: 17103206]
- Houk JC. Participation of reflex mechanisms and reaction time processes in the compensatory adjustments to mechanical disturbances. *Prog Clin Neurophysiol*. 1978; 4:193–215.
- Keen DA, Fuglevand AJ. Distribution of motor unit force in human extensor digitorum assessed by spike-triggered averaging and intraneural microstimulation. *J Neurophysiol*. 2003; 91:2515–2523. [PubMed: 14724266]
- Kilbreath SL, Gandevia SC. Limited independent flexion of the thumb and fingers in human subjects. *J Physiol*. 1994; 479:487–497. [PubMed: 7837104]
- Kim SW, Shim JK, Zatsiorsky VM, Latash ML. Anticipatory adjustments of multi-finger synergies in preparation for self-triggered perturbations. *Exp Brain Res*. 2006; 174:604–612. [PubMed: 16724179]
- Klous M, Danna-dos-Santos A, Latash ML. Multi-muscle synergies in a dual postural task: Evidence for the principle of superposition. *Exp Brain Res*. 2010; 202:457–471. [PubMed: 20047089]
- Lang CE, Schieber MH. Human finger independence: limitations due to passive mechanical coupling versus active neuromuscular control. *J Neurophysiol*. 2004; 92:2802–2810. [PubMed: 15212429]
- Latash, ML. *Synergy*. New York: Oxford University Press; 2008.
- Latash ML. Motor control: In search of physics of the living systems. *J Hum Kinet*. 2010; 24:7–18.
- Latash ML. Motor synergies and the equilibrium-point hypothesis. *Motor Control*. 2010; 14:294–322. [PubMed: 20702893]
- Latash ML, Friedman J, Kim SW, Feldman AG, Zatsiorsky VM. Prehension synergies and control with referent hand configurations. *Exp Brain Res*. 2010; 202:213–229. [PubMed: 20033397]
- 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; 122:131–138. [PubMed: 9776511]
- Latash ML, Scholz JF, Danion F, Schoner G. Structure of motor variability in marginally redundant multifinger force production tasks. *Exp Brain Res*. 2001; 141:153–165. [PubMed: 11713627]
- Latash ML, Scholz JP, Schöner G. Motor control strategies revealed in the structure of motor variability. *Exerc Sport Sci Rev*. 2002; 30:26–31. [PubMed: 11800496]
- Latash ML, Scholz JP, Schöner G. Toward a new theory of motor synergies. *Motor Control*. 2007; 11:276–308. [PubMed: 17715460]

- Latash ML, Zatsiorsky VM. Multi-finger prehension: control of a redundant mechanical system. *Adv Exp Med Biol.* 2009; 629:597–618. [PubMed: 19227523]
- Leijnse JNAL. Measuring force transfers in the deep flexors of the musician's hand: theoretical analysis, clinical examples. *J Biomech.* 1997; 30:873–882. [PubMed: 9302609]
- Li S, Latash ML, Zatsiorsky VM. Finger interaction during multi-finger tasks involving finger addition and removal. *Exp Brain Res.* 2003; 150:230–236. [PubMed: 12669172]
- Li ZM, Dun S, Harkness DA, Brininger TL. Motion enslaving among multiple fingers of the human hand. *Motor Control.* 2004; 8:1–15. [PubMed: 14973334]
- Li ZM, Latash ML, Zatsiorsky VM. Force sharing among fingers as a model of the redundancy problem. *Exp Brain Res.* 1998; 119:276–286. [PubMed: 9551828]
- Liddell EGT, Sherrington CS. Reflexes in response to stretch (myotatic reflexes). *Proc Roy Soc London Ser B.* 1924; 96:212–242.
- Magnusson SP. Passive properties of human skeletal muscle during stretch maneuvers. A review. *Scand J Med & Sci Sport.* 1998; 8:65–77.
- Martin JR, Latash ML, Zatsiorsky VM. Interaction of finger enslaving and error compensation in multiple finger force production. *Exp Brain Res.* 2009; 192:293–298. [PubMed: 18985331]
- Martin JR, Budgeon MK, Latash ML, Zatsiorsky VM. Stabilization of the total force in multi-finger pressing tasks studied with the 'inverse piano' technique. *Hum Move Sci.* 2010 (In Press).
- Matthews PBC. The dependence of tension upon extension in the stretch reflex of the soleus of the decerebrate cat. *J Physiol.* 1959; 47:521–546. [PubMed: 16992028]
- McNulty PA, Cresswell AG. Recruitment of single human low-threshold motor units with increasing loads at different muscle lengths. *J Electromyography Kinesiol.* 2004; 14:369–377.
- Merton, PA. *The Spinal Cord.* Boston: Little, Brown; 1953. Speculations on the servo control of movement; p. 183-198.
- Olafsdottir H, Yoshida N, Zatsiorsky VM, Latash ML. Anticipatory covariation of finger forces during self-paced and reaction time force production. *Neurosci Lett.* 2005; 381:92–96. [PubMed: 15882796]
- Olafsdottir H, Yoshida N, Zatsiorsky VM, Latash ML. Elderly show decreased adjustments of motor synergies in preparation to action. *Clin Biomech.* 2007; 22:44–51.
- Olafsdottir H, Kim SW, Zatsiorsky VM, Latash ML. Anticipatory synergy adjustments in preparation to self-triggered perturbations in elderly individuals. *J Appl Biomech.* 2008; 24:175–179. [PubMed: 18579910]
- Rack PMH, Westbury DR. The effects of length and stimulus rate on tension in the isometric cat soleus muscle. *J Physiol.* 1969; 204:443–460. [PubMed: 5824646]
- Rathelot JA, Strick PL. Muscle representation in the macaque motor cortex: An anatomical perspective. *PNAS.* 2006; 103:8257–8262. [PubMed: 16702556]
- Sanes JN, Donoghue JP, Thangaraj V, Edelman RR, Warach S. Shared neural substrates controlling hand movements in human motor cortex. *Science.* 1995; 268:1775–1777. [PubMed: 7792606]
- Schieber MH. Muscular production of individuated finger movements: the roles of extrinsic finger muscles. *J Neuroscience.* 1995; 15:284–297.
- Schieber MH, Hibbard LS. How somatotopic is the motor cortex hand area. *Science.* 1993; 261:489–492. [PubMed: 8332915]
- Schieber MH, Santello M. Hand function: peripheral and central constraints on performance. *J Appl Physiol.* 2004; 96:2293–2300. [PubMed: 15133016]
- Scholz JP, Danion F, Latash ML, Schoner G. Understanding finger coordination through analysis of the structure of force variability. *Biol Cybern.* 2002; 86:29–39. [PubMed: 11918210]
- Scholz JP, Schöner G. The uncontrolled manifold concept: Identifying control variables for a functional task. *Exp Brain Res.* 1999; 126:289–306. [PubMed: 10382616]
- Schöner G. Recent developments and problems in human movement science and their conceptual implications. *Ecol Psychol.* 1995; 8:291–314.
- Shapkova EY, Shapkova AL, Goodman SR, Zatsiorsky VM, Latash ML. Do synergies decrease force variability? A study of single-finger and multi-finger force production. *Exp Brain Res.* 2008; 188:411–425. [PubMed: 18425506]

- Shim JK, Park J, Zatsiorsky VM, Latash ML. Adjustments of prehension synergies in response to self-triggered and experimenter-triggered load and torque perturbations. *Exp Brain Res*. 2006; 175:641–653. [PubMed: 16804720]
- Vigouroux L, Ferry M, Colloud F, Paclet F, Cahouet V, Quaine F. Is the principle of minimization of secondary moments validated during various fingertip force production conditions? *Hum Mov Sci*. 2008; 27:396–407. [PubMed: 18400321]
- Zatsiorsky VM, Gregory RW, Latash ML. Force and torque production in static multifinger prehension: biomechanics and control. II. Control. *Biol Cybern*. 2002; 87:40–49. [PubMed: 12111267]
- Zatsiorsky VM, Latash ML. Multi-finger prehension: An overview. *J Mot Behav*. 2008; 40:446–476. [PubMed: 18782719]
- Zatsiorsky VM, Li ZM, Latash ML. Coordinated force production in multi-finger tasks: Finger interaction and neural network modeling. *Biol Cybern*. 1998; 79:139–150. [PubMed: 9791934]
- Zatsiorsky VM, Li ZM, Latash ML. Enslaving effects in multi-finger force production. *Exp Brain Res*. 2000; 131:187–195. [PubMed: 10766271]
- Zhang W, Scholz JP, Zatsiorsky VM, Latash ML. What do synergies do? Effects of secondary constraints on multi-digit synergies in accurate force-production tasks. *J of Neurophys*. 2008; 99:500–513.

Figure 1. Top and side view of force transducer set up. Transducers were equally spaced laterally and adjustable in the forward/backward direction. Each transducer was rigidly attached to a linear actuator.

Figure 2.

Examples of trials. A. MVC trial (I-Finger). B. Ramp-target trial (I-Finger). C. Experimental trial as the feedback appeared to the subject (I-Finger). D. Finger force data during experimental trial (I-Finger).

Figure 3.

ΔF and ΔMD changes as a function of proximity from target finger for: A) *Invol* and B) *Vol*. Asterisks (*) indicate a significant difference between ΔF and ΔM values. Error bars are SE.

Figure 4. ΔF and ΔMD during the involuntary phase (finger lifting) for target fingers: A) I-Finger, B) M-finger, C) R-finger, and D) L-finger. Asterisk (*) indicates a significant difference between ΔF and ΔMD of a finger.

Figure 5. Δ F and Δ MD during the voluntary phase (finger pressing) for target fingers: A) I-Finger, B) M-finger, C) R-finger, and D) L-finger. Asterisk (*) indicates a significant difference between Δ F and Δ MD of a finger.

Table 1

One-way repeated measures ANOVA results.

A)										
Response Type	Factor	Involuntary Response								
		Target Finger			Non-Target Fingers			Total		
		DOF	F	p	DOF	F	p	DOF	F	p
ΔF	Finger	2.152	3.037	0.043	2.573	9.312	0.000	2.031	6.738	0.005
ΔMD	Finger	2.275	9.973	0.000	1.905	8.781	0.000	3.000	12.837	0.000

B)										
Response Type	Factor	Voluntary Response								
		Target Finger			Non-Target Fingers			Total		
		DOF	F	p	DOF	F	p	DOF	F	p
ΔF	Finger	3.000	4.779	0.007	2.311	10.435	0.000	1.943	13.691	0.000
ΔMD	Finger	3.000	8.579	0.000	2.433	2.463	0.095	3.000	5.278	0.004

Note: The effect of Finger on ΔF and ΔMD is given for the involuntary phase (passive finger lifting) and voluntary phase (finger pressing). DOF stands for degrees-of-freedom corrected for violations of sphericity.

Table 2

Mean moment produced about NL by perturbed finger and all fingers ($\pm$ SE). A) Involuntary phase. B) Voluntary phase.

A)				
<i>Target Finger</i>	Δ Target Finger Moment		Δ Total Moment	
	<i>F</i>	<i>MD</i>	<i>F</i>	<i>MD</i>
I	170.35 $\pm$ 15.89	154.35 $\pm$ 15.47	101.70 $\pm$ 12.58	73.90 $\pm$ 26.36
M	-23.64 $\pm$ 10.75	-30.96 $\pm$ 13.92	-48.12 $\pm$ 12.53	-42.04 $\pm$ 20.89
R	-12.74 $\pm$ 6.83	-19.27 $\pm$ 9.47	-74.22 $\pm$ 7.25	-132.86 $\pm$ 28.96
L	-17.16 $\pm$ 8.17	-26.57 $\pm$ 12.20	-149.36 $\pm$ 19.16	-128.33 $\pm$ 36.71

B)				
<i>Target Finger</i>	Δ Target Finger Moment		Δ Total Moment	
	<i>F</i>	<i>MD</i>	<i>F</i>	<i>MD</i>
I	527.38 $\pm$ 77.37	561.40 $\pm$ 96.15	354.68 $\pm$ 71.22	410.71 $\pm$ 117.81
M	-807.03 $\pm$ 93.47	-1037.31 $\pm$ 192.22	49.99 $\pm$ 44.39	-164.55 $\pm$ 84.79
R	-812.61 $\pm$ 75.15	-1287.41 $\pm$ 230.55	-329.29 $\pm$ 55.05	-652.09 $\pm$ 156.99
L	-752.51 $\pm$ 89.90	-1281.54 $\pm$ 195.35	-421.21 $\pm$ 72.59	-1041.90 $\pm$ 212.47

Note: Moments were computed based on F and MD values. Units of moment are Nmm.