Published in final edited form as:

Exp Brain Res. 2008 September ; 190(2): 225–238. doi:10.1007/s00221-008-1466-x.

Stability of the multi-finger prehension synergy studied with transcranial magnetic stimulation

Xun Niu, Vladimir M. Zatsiorsky, and Mark L. Latash

Department of Kinesiology, The Pennsylvania State University

Abstract

We used transcranial magnetic stimulation (TMS) to explore the stability of the three constituents of the multi-finger prehension synergy. Patterns of co-variation between mechanical variables produced by individual digits were used as indices of the prehension synergy. We tested hypotheses that TMS would violate these patterns and that different components of the prehension synergy would take different times to restore. Subjects held an instrumented handle with one of the three external load and one of the seven external torques statically in the air. Single-pulse TMS was applied unexpectedly over the hand projection in the contralateral hemisphere. The normal forces showed a quick TMS-induced increase that was proportional to the background force magnitude. This was also true for the tangential forces produced by the thumb, middle and ring fingers but not by the index and little fingers. The total moment of force changed proportionally to its background value with predominance of supination responses. During the quick force response to TMS, patterns of digit force co-variation stabilizing the total tangential force and total moment of force were violated. Two stages of synergy restoration were identified taking approximately 0.3 s and 1.5 s. These times differed among the three synergy components. The results support the idea of a prehension synergy as a neural mechanism that facilitates conjoint changes in forces produced by individual digits with the purpose to stabilize the hand action on the hand-held object. The data also support applicability of the principle of superposition to the human hand action.

Keywords

prehension; synergy; transcranial magnetic stimulation; hand; principle of superposition

Introduction

Recent studies of multi-finger manipulation of hand-held objects (prehension) have been based on an assumed two-level hierarchical control scheme (reviewed in Arbib et al. 1985; Mackenzie and Iberall 1994). At the upper level of the hierarchy, the task (required mechanical action on the hand-held object) is distributed between the thumb and a virtual finger (VF) - an imagined finger with the mechanical action equal to that of the four fingers of the hand. At the lower level, action of the VF is distributed among individual fingers. At both levels, patterns of conjoint changes in forces and moments of force produced by the digits have been documented, addressed as prehension synergies (reviewed in Zatsiorsky and Latash 2004, 2008; Latash et al. 2007).

Three main constituents of prehension synergies have been described at the thumb-VF level related to the production of (a) internal forces, i.e. the forces that cancel each other and hence

do not disturb the object equilibrium, e.g., the grip force (Kerr and Roth 1986; Yoshikawa and Nagai 1991; Gao et al. 2005), (b) resultant force; and (c) resultant moment of force acting on the object. In tasks of holding an object oriented vertically using a prismatic grasp (the thumb opposing the four fingers), the three constituents can be expressed as:

$$\begin{aligned} f_{vf}^n + f_{th}^n &= 0 \\ f_{vf}^t + f_{th}^t &= F_{LOAD} \\ M^t + M^n &= M_{EXT} \end{aligned} \quad (1)$$

where f is force, M is moment of force, M_{EXT} is external moment of force, superscripts t and n refer to tangential and normal forces and moments produced by those forces, and subscripts vf and th stand for the VF and the thumb, respectively. Patterns of co-variation between the two summands on the left-hand side of the three equations have been used as signatures of corresponding synergy components (Shim et al. 2003, 2004; Gao et al. 2006). Note that the equations can be satisfied with sufficient accuracy without such co-variations (synergies), for example by selecting values of the summands in the left sides and keeping their variability very low. A number of studies have suggested that the synergies ensuring a stable value of the grip force and a stable rotational equilibrium are controlled using the principle of superposition introduced for the hand action in robotics (Arimoto et al. 2001; Zatsiorsky et al. 2004). According to this principle, two separate commands define the grip force and the total moment of force, respectively, and digit variables defined by the two commands are summed up.

In this paper, we address issues of stability of prehension synergies. For this purpose, we used, as the source of perturbation, single-pulse transcranial magnetic stimulation (TMS) applied over the hand projection in the contralateral primary motor cortex. Muscles with higher background activation levels are known to show larger responses to TMS (Ravnborg et al. 1991; Lim and Yiannikas 1992; Cros et al. 2007). Hence, when a digit produces a pressing force, a single TMS stimulus leads to a short-latency increase in the force (Danion et al. 2003) possibly mediated by descending signals in the corticospinal tract (Ugawa et al. 1995; Classen et al. 1998). The force increase is followed by a delayed drop in the force associated with a silent period in the activity of extrinsic hand flexors (Danion et al. 2003). TMS has also been hypothesized to interrupt motor planning processes; this hypothesis was based, in particular, on observations of changes in reaction time produced by a TMS pulse (Day et al. 1989; Pascual-Leone et al. 1992; Berardelli et al. 1994; van der Kamp et al. 1998).

A TMS applied during a task of holding an object statically in the air may be expected to lead to changes in the overall mechanical action of the hand on the object such as the grip force and tangential force. The stimulus may also be expected to affect the prehension synergy, that is, it may be expected to violate equations (1). To our knowledge, no studies of effects of TMS on patterns of digit force co-variation (multi-digit synergies) during prehensile tasks have been performed. A report on a pilot study of the effects of TMS on digit forces in the tripod grasp mentions different effects of the TMS on the grasp force and the net force (Baud-Bovy et al. 2005, 2008). Another study has shown that the TMS-induced muscle responses are sensitive to precision demands during two-digit precision grip tasks (Bonnard et al. 2007). One more recent study (Cros et al. 2007) has reported high correlations between the direction of TMS-induced force responses and the direction of voluntary forces, while the magnitude of the responses depended strongly on the rate of voluntary force production. These authors have also reported different timing of the responses in agonist and postural muscles and concluded that TMS does not disrupt the “architecture of motor plans” (Cros et al. 2007). If one considers synergies to be a major part of the “architecture of motor plans”, they are expected to be preserved following TMS. In contrast, we expected the synergy constituents, i.e. the co-variations between the summands on the left-hand side of the equations (1), to be violated by a TMS and take time to restore. Documenting such violations would provide a strong argument that neural circuitry responsible for the co-variation patterns characteristic of the prehension

synergy is located upstream of the stimulation site (M1 cortical area). Indeed, if this circuitry were located downstream, TMS would lead to a change in an input signal into the synergy-forming circuitry, and synergies may be expected to persist. Based on the principle of superposition, we also expect different time patterns of restoration of the synergy constituents corresponding to each of the three equations (1).

Methods

Subjects

Six male subjects participated in the experiment (age 28.7 ± 2.5 years, weight 73 ± 15.2 kg, height 1.75 ± 0.07 m, hand length from the middle fingertip to the distal crease of the wrist with hand extended 19.1 ± 1.5 cm, hand width at the MCP level with hand extended 10.3 ± 0.8 cm). The subjects were all right-hand dominant and had no history of neuropathy or trauma to their upper limbs and their heads. All subjects gave informed consent according to the procedures approved by the Office for Research Protections of the Penn State University.

Apparatus

Five six-component force/moment transducers (Nano-17, ATI Industrial Automation, Garner, NC, USA) were mounted on an aluminum handle at the bottom of which a horizontal aluminum bar was attached (0.8 m long, Figure 1). A level was positioned at the top of the handle to help the subjects keep the handle vertical. Four transducers were used to measure forces and moments of force applied by the fingers, and the fifth transducer measured the force and moment of force produced by the thumb. The surface of each sensor was covered with sandpaper (friction coefficient about 1.4, see Shim et al. 2003; Savescu et al. 2008). The centers of all five sensors were in one plane (the grasp plane). Sensor signals were set to zero prior to each trial.

The distance between two finger sensors was 3.0 cm, and the thumb sensor was positioned across the midpoint between the centers of the middle and ring finger sensors. The combined mass of the handle, sensors, and the bar was 0.58 kg. Three loads, 0.25 kg, 0.5 kg, and 0.75 kg, could be attached at different points along the bar. Their suspension at different locations generated seven external torques: 0.2 Nm, 0.4 Nm and 0.6 Nm clockwise and counterclockwise, as well as a zero torque. There were a total of 21 different load/torque conditions in the experiment.

Bipolar electromyographic (EMG) recordings from flexor digitorum superficialis (FDS) and extensor digitorum communis (EDC) of the right forearm were obtained from pairs of Ag/AgCl surface electrodes. The ground reference electrode was placed on the subject's styloid process of the ulna. The diameter of each electrode was 1 cm, the distance between the centers of two electrodes was 3 cm. EMG electrode positions were secured by tape. Bortec 8-channel electromyographic (EMG) system (AMT-8, Bortec Biomedical Ltd, Calgary, Alberta, Canada) was used to acquire and transmit EMG signals to the computer. The gain of the EMG amplifier was set at 5K. Since this study has focused on mechanical responses to TMS, the EMG signals were only used to define the time when TMS occurred (Figure 3A).

All the signals were digitized by two 32-channel 12-bit A/D converters (PCD-6033E, National Instruments, Austin, TX, USA). The sampling frequency was 1000 Hz. The digital signals were processed by a PC computer (Dell Dimension 8200, USA) with a customized program written in LabVIEW 6.1 (National Instruments, Austin, TX, USA).

TMS procedure

Focal TMS was delivered with a Magstim-200 stimulator (Magstim, Wales, UK) with a 70-mm figure-of-eight coil (P/N 9925-00), which produced a monophasic magnetic field with the maximal output of 1.7 Tesla reached in 0.5 ms and decaying over approximately 1 ms.

The subject put on a Nylon swimming cap, which was fixed bilaterally on the subject's scalp with tape to avoid its motion during the experiment. A 10×10 grid with the step of 0.5 cm was marked on the lateral-anterior left side of the cap. The subject was first instructed to be relaxed, and then TMS stimuli at 70% of maximal power were applied over the subject's left motor cortex. The coil was oriented at about 30° over the transverse plane with the handle pointing forward. The experimenter systematically changed the location of the central point of the coil over the grid and observed the response of the subject's digits, which rested naturally on the table. An optimal position of the coil was defined as the spot with the largest magnitude of the digit response. Typically, the optimal position was about 2 cm anterior and 3 cm lateral of Cz, and varied among subjects within 1 cm. During the experiment, the center of the coil was always placed at the optimal location. The coil was fixed onto the swimming cap by double-sided adhesive tape and also held by an experimenter to avoid fatigue to the subject and ensure that the coil position and orientation were constant across trials.

To determine the stimulation intensity, the output of the stimulator was reduced gradually until no visible response to a single TMS could be observed in three of six consecutive stimulations. This intensity was viewed as the resting motor threshold (rMT). Since we have been interested in the combined mechanical effects of the TMS-induced responses in many muscles, a mechanical rather than electromyographic criterion has been selected for rMT. Then, the output was set as 140% of rMT. The stimulation strength ranged from 55% to 72% of the stimulator output and had an average of 65% across subjects.

Experimental Procedure

Before the experiment, subjects were given an orientation session to familiarize them with the experimental tasks and apparatus. Then, subjects washed their hands to normalize skin condition. The subject sat in a chair alongside a table, with the right upper arm positioned at approximately 45° abduction in the frontal plane and 30° flexion in the sagittal plane. The elbow joint was flexed by approximately 90° . The forearm, but not the wrist and hand, was placed on the brace. The brace was fastened to the table and the forearm was fixed in the brace with an elastic band. The forearm was pronated 90° such that the hand was in a natural grasping position.

Subjects were instructed to take the handle from the rack and keep the handle vertically and statically in the air while looking at the air bubble level. When the handle was stabilized, the trial started, and a TMS stimulus was applied at an unpredictable time during the first 4 s; the subjects had sufficient time (at least 2 s) to re-stabilize the handle. The instruction to the subjects was: "Try to keep the handle vertical at all times". After the data collection in a trial stopped, the subjects placed the handle back on the rack and waited for the next trial.

In further text, different load/torque combinations are also addressed as load/torque conditions. The order of loads and torques was randomized, while three trials were presented in a row within each load/torque condition. After the third trial, the load and/or the location of the load along the bar was changed by the investigator. Each trial took 6 seconds. A 30-s break was provided after each trial within a load/torque condition, and at least 3-min breaks were provided between two consecutive conditions. The total duration of the experiment was approximately 1.5 hours.

Data analysis

Software written in LabView (National Instruments, NC, USA) was used to convert digital signals into the force and moment of force values. Data processing was performed using Matlab software package (Mathworks, In., Natick, MA, USA). The raw force/moment data were filtered with a fourth-order, zero-lag Butterworth low-pass filter at 12.5 Hz.

In further text, symbols m and f designate a digit's moment of force and force, respectively. Subscript i refers to the i th digit, such as the thumb (th), index (in), middle (mi), ring (r) and little finger (l). Subscript vf is for the virtual finger. VF force was computed as the sum of forces produced by the four fingers. Superscripts x , y , or z represent the axes with respect to which the force or moment were determined. In the transducer-fixed reference system, forces normal to the transducer surface corresponded to the z direction f^z . In this experiment, f^z was oriented horizontally. At equilibrium states, the tangential force acted in the vertical direction f^y .

The digit contacts with the sensors were modeled as soft-finger contacts (Murray et al. 1994); in particular rolling and deforming the fingertips were allowed. The vertical coordinates (y_i) of the digit force application (point P in the right panel in Figure 1) with respect to the sensor center were computed as $y_i = (m_i^x \pm f_i^y \times d) / f_i^z$, $i = 1, 2, 3, 4, 5$ and plus-minus sign depends on the digit: minus for the thumb; plus for the index, middle, ring and little fingers, m_i^x is the moment of the i th digit with respect to x -axis (horizontal axis), f_i^y and f_i^z are the forces of the i th digit in the y and z directions, $d = 0.5$ cm is the sensor cap height, i.e. the distance between the fingertip contact and the sensor.

The vertical coordinate of the point of VF normal force application with respect to the point of application of the thumb force was determined based on the theorem of moments as

$Y_{vf} = \sum f_i^n Y_i / f_{vf}^n$, where Y_i is the vertical coordinate of the force application point of finger i . Y_i equals the algebraic sum of (1) the vertical coordinate of the sensor center in the handle fixed reference system (e.g. 1.5 cm for the index finger and -1.5 cm for the middle finger, see Figure 1), (2) the displacement of the point of application of the thumb force with respect to the center of the thumb sensor, and (3) y_i , the displacement of the application point of the finger i 's normal force with respect to the sensor center. f_{vf}^n is the sum of the normal forces produced by the four fingers. Note that a capital letter, such as Y , is used to designate a coordinate in the handle fixed reference system, while the lowercase letter like y designates the coordinate with respect to the center of a sensor.

At the VF level, the moment of normal forces M^n and the moment of the tangential forces M^t were computed. The moment of normal forces was computed as $M^n = f_{vf}^n \times Y_{vf}$, and the moment of tangential forces was computed as $M^t = (f_{vf}^t - f_{th}^t) w / 2$, where w is the width of the handle (76 mm). M^n is the moment produced by the force couple consisting of the thumb and VF normal forces; it can be computed using either the normal force of the thumb or the normal force of the VF (as in the expression above). Because the moment of a couple is a free moment, M^n can be added to M^t to obtain the total moment exerted by the subject. Upward tangential forces and counterclockwise moments were defined as positive. Background values of all the force and moment of force variables were computed as their average values over the time interval from 300-100 ms prior to the TMS application.

Synergy restoration analysis

The concept of equilibrium restoration—We introduce the concept of equilibrium restoration using an example. When the time changing tangential forces of the thumb and VF

were plotted against each other (Figure 2B), the following regularities in the force-force relations have been observed:

1. Prior to the TMS, simultaneous synchronous variations of the VF and thumb force magnitudes were always present (the red traces in Figure 2B). Such conjoint matching changes of the thumb and VF tangential forces manifest a constituent of the grasping synergy (Zatsiorsky and Latash 2004).
2. Immediately after the TMS (the green portion of the force-force curve in Figure 2B) the forces of the thumb and index finger changed in a less regular way such that $f_{vf}^t + f_{th}^t \neq -Load$ and hence the handle equilibrium in the vertical direction was broken.
3. After some time the resultant tangential force approximated in magnitude *Load* again (the blue curve in Figure 2B). The handle equilibrium was restored but the force magnitudes varied substantially. We can say that the tangential force synergy has been restored.
4. The forces magnitudes stabilized at a certain steady-state level (the black portion of the line in Figure 2B).

Figures similar to Figure 2B can be drawn for the TMS-induced changes in the normal forces (Figure 2A) that are supposed to sum up to zero and moments of force produced by the tangential and normal forces (Figure 2C) that are supposed to sum up to the external torque. The following formal definitions of the normal force synergy (grasping synergy), tangential force synergy, and the moment-of-force synergy are adopted here:

- A. Normal force synergy is defined as co-variation of the normal forces of the thumb and VF that satisfies the equation:

$$f_{vf}^n + f_{th}^n = 0 \quad (2)$$

- B. Tangential force synergy is defined as co-variation of the tangential forces of the thumb and VF that satisfies the equation:

$$f_{vf}^t + f_{th}^t = F_{LOAD} \quad (3)$$

where F_{LOAD} is the force produced by the subject that supports the weight of the object ($F_{LOAD} = -Load$).

- C. Moment of force synergy is defined as co-variation of the moments produced by the normal and tangential forces that satisfies the equation:

$$M^{tot} = M^n + M^t = M_{EXT} \quad (4)$$

where M^{tot} , M^n , M^t are the total moment of force, moment of normal forces and moment of tangential forces exerted by the subject, respectively.

Based on the patterns illustrated in Figure 2, synergy restoration was viewed as consisting of two stages, Stage-1 (synergy is restored in a sense that force and moment of force co-variations satisfy equations 2-4; however, force and moment of force magnitudes produced by the thumb and VF continue to change substantially) and Stage-2 (a new steady-state is reached). An operational definition for the two stages is described in the following section.

Search methods for the timing of synergy restoration—Let us introduce a notion of the *equality line* as a line corresponding to one of the equations (2) - (4). If data points measured at different time samples stay close to the equality line, they satisfy the corresponding synergy. The following computational steps were selected to estimate time changes in two variables: (1) The distances of the data points from the equality line; and (2) The differences between the

magnitudes of force and moment of force produced by the thumb and VF at different times after the TMS and those values measured at a steady-state after the handle was at a new equilibrium. This particular method was based on many trial-and-error attempts and analysis of the data for each individual subject. These steps lead to the most consistent across subjects and conditions results.

First, the distance from each point of the data to the equality line (for example, the distance from each data point on the plane spanned by the VF and thumb normal forces to the corresponding equality line) was calculated. This variable is shown in Figure 3B as $\text{Dist}(t)$. The maximal distance from the last 200 data points to the equality line was accepted as the *steady-state distance* (Δ_{SS}).

Second, the standard deviation (SD) of the performance variable of interest was calculated within a moving window of 50 ms. By moving the window 1 ms at a time, a time series $\text{SD}(t)$ was computed (Figure 3B). We used the 50 ms time window as a compromise between having sufficient statistical power and sufficient time resolution. The root mean square (RMS) over 200 points at the end of each SD time series was computed; it was termed the *steady-state standard deviation* (SD_{SS}). The indices Δ_{SS} and SD_{SS} characterize the typical for this subject variations in the mechanical variables at the new steady-state. In some of the subjects, visual analysis of the data clearly showed two stages in the process of equilibrium restoration (seen in Figure 3); other subjects showed a more smooth, less staged process. To test whether these processes differed across the three performance variables corresponding to equations (2)-(4), we decided to view them as consisting of two stages across all subjects.

I. The forward propagation method: Stage-1.

The search process started from the time when the TMS occurred, which was defined using the EMG recording (time zero, $T=0$) and moved along the natural time. If, after a certain time, the RMS computed over 100 points in $\text{SD}(t)$ was under 10SD_{SS} , and the maximal value of $\text{Dist}(t)$ over those 100 consecutive data point was under $10\Delta_{SS}$, this time (T_1) was regarded as the beginning of Stage-1.

II. The backward propagation method: Stage-2.

The search process started from the end of the SD time series and moved in the backward direction, i.e. opposite to the natural time sequence. The last point, for which the RMS value of 100 consecutive points in $\text{SD}(t)$ was smaller than 3SD_{SS} , and the maximal value of $\text{Dist}(t)$ over those 100 consecutive data points was smaller than $3\Delta_{SS}$, was regarded as the end of Stage-1 and start of Stage-2 (T_2). An illustration of T_1 and T_2 is presented in Figure 3 with the corresponding normal force, $\text{Dist}(t)$, and $\text{SD}(t)$ series.

Statistical analysis

All the data were averaged over the three trials at each condition. ANOVA with and without repeated measures and paired Student's t-tests were used. The factors included *Load* (three levels), *Torque* (seven levels), *Condition* as a factor (21 levels corresponding to all the external Load-Torque combinations, used only for the synergy restoration analysis), and *Finger* (four levels). Significant effects were further explored using Tukey's pair-wise comparisons.

The significance level was set as 0.05. Statistical analyses were performed in Minitab 13.0 (Minitab, Inc., State College, PA, USA) and SPSS (SPSS Inc., Chicago, IL, USA).

To check the data for accuracy, the following comparisons have been regularly performed for all trials: (a) the normal forces of the thumb and VF at equilibrium should add up to zero; (b) the total tangential force at equilibrium should equal the weight of the object; (c) the total

moment of force should counterbalance the external torque; and (d) the EMG recordings should show a motor evoked potential (MEP), a silent period and return to about the pre-TMS level.

Results

This section is organized in the following way. First, we analyze the behavior prior to the TMS. Further, we illustrate typical effects of TMS on digit forces. Then, we analyze the immediate effects of TMS on the grip force, tangential force, and total moment of force. Finally, the time course of the restoration of equilibrium after a TMS is described.

Behavior prior to the stimulation

All the subjects showed co-variation among digit forces and moments of force that satisfied the equilibrium equations (1). In particular, there was positive co-variation of the normal forces produced by the thumb and virtual finger (VF). This relation is illustrated by the red dots in Figure 2A for a typical subject holding a load of 0.75 kg with the external torque of - 0.4 Nm. There was negative co-variation between the tangential forces of the thumb and VF (Figure 2B) and also between the moment of normal forces and the moment of tangential forces (Figure 2C). Overall, the average amount of variance prior to the TMS accounted for by the linear equations was 97.1%, 85.5%, and 73.2% for the grip force, tangential force, and total moment of force respectively.

Typical patterns of the TMS-induced changes

The individual digit forces (including VF force), the total force and the moment of force are shown as time functions in Figure 4 for a typical trial performed by a representative subject. Overall, the digit forces stabilized within one-two seconds after the TMS but all subjects showed variable patterns of transient changes in all the digit forces. Four phases can be distinguished in the normal force changes (panels A in Figure 2 and Figure 4):

1. **Fast Force Increase (FFI):** The average latency of the early response (motor evoked potential, MEP) in the FDS was 17.4 ± 1.9 ms (SD is across all conditions). Immediately following a TMS, at a latency of about 25 ± 4 ms, the VF normal force f_{vf}^n and thumb normal force f_{th}^n both increased rapidly and reached maximum values at about the same time. The average time to peak force, T_p , was 67.0 ± 9.57 ms. Two-way repeated-measures ANOVA with the factors *Load* and *Torque* showed no significant effects on T_p . f_{vf}^n increased slightly faster than the thumb normal force f_{th}^n . In all the subjects and under all conditions, the force-force line was above the line of equal force changes, as in Figure 2A.
2. **Fast Force Decrease (FFD):** After reaching the peak values, both forces dropped along a nearly straight line on the force-force plane, but f_{vf}^n dropped slightly faster than f_{th}^n getting closer to the force equality line. A linear regression model was fitted for the FFI and FFD phases separately in each trial. The R-squared values averaged over all subjects and conditions were 99% and 96.7% for FFI and FFD respectively. Two-way repeated measures *Load* $\times$ *Torque* ANOVAs were run on the regression coefficients; no significant effects were found.
3. **Irregular Pattern Phase:** After the FFD phase, there was a period of irregular force changes, ultimately leading close to the equality line.
4. **Synergy Restoration:** Later, the force changes were mainly along the equality line, i.e. they satisfied the equation of statics (equation (2) in Methods). While f_{vf}^n and f_{th}^n were nearly equal both prior to and after TMS, the magnitude of these forces was larger after TMS, i.e. the handle was grasped stronger.

The relation between the TMS-induced changes in the VF and thumb tangential forces, f_{vf}^t and f_{th}^t , showed a less regular pattern (illustrated earlier in Figure 2B). Right after the TMS, the handle could move up and down (or down and up) until the force-force relation came close to the equality line (shown as the straight dashed line with a negative slope in Figure 2B) corresponding to equation (3) in Methods.

The balance of moments of force was also violated by the TMS, but then it gradually went close to and finally settled down along the moment equality line corresponding to equation (4) in Methods (Figure 2C).

Early Force Changes after TMS

In order to simplify the analysis, the forces and moments of force were measured when the normal force peak value was reached. Then, they were compared to the steady-state values prior to the TMS (averaged over the time interval 300-100 ms prior to TMS application, see Methods). The changes of forces and moments of force during this period were monotonic. In the ensuing description of the changes in the tangential forces, the upward direction is considered positive. The following force and moment changes were observed.

All digit normal forces increased (described earlier, Figure 2A). The thumb tangential force increased in 366 out of the total of 378 trials. Eleven of the 12 trials with a decrease in f_{th}^t were produced by one subject. The TMS-induced change of this force Δf_{th}^t was significantly affected by the direction of the rotational effort (Table 1) such that Δf_{th}^t during the supination effort conditions was larger than in the conditions with no rotation effort, while it was the smallest in the pronation effort conditions.

The percentage of trials with positive f_{vf}^t depended on the external torque (Table 1). There were more cases of positive Δf_{vf}^t in trials with pronation efforts as compared to trials with supination efforts. The magnitude of Δf_{vf}^t was affected by external torque. However, this effect was opposite to the one for Δf_{th}^t (Table 1). During conditions with pronation efforts Δf_{vf}^t was larger than during tasks with zero rotation effort, while Δf_{vf}^t was the smallest during the supination effort conditions. The change in the total tangential force is also shown in Table 1. There was no significant effect of *Torque* or *Load* and no interaction.

The TMS-induced change in the total moment of force, ΔM^{tot} depended on whether the effort prior to the TMS was into supination or into pronation. The percentage of trials with negative ΔM^{tot} for each external torque is shown in Figure 5. Negative ΔM^{tot} signify an increase in the supination effort or a decrease in the pronation effort. In the supination effort conditions (positive external torque), in over 90% of the trials the total moment changed into supination. Under zero external torque conditions, ΔM^{tot} was into supination in about 65% of the trials, and in the pronation effort conditions, ΔM^{tot} was into supination in about 50% of the trials.

Quantitative analysis of the TMS-induced responses

The TMS-induced normal force increment during the FFI period showed an overall tendency to increase with the background force. The relations between the increment of individual digit's force value and background normal force in each individual subject could be described by a linear regression model, which accounted, on average, for over 70% of the variance for each digit. However, the slopes of the force-force regression line (regression coefficient) differed across digits and subjects; their average values across subjects were 0.40 ± 0.16 , 0.19 ± 0.07 , 0.48 ± 0.24 , 0.63 ± 0.25 and 0.59 ± 0.30 for the thumb, index, middle, ring and little finger,

respectively. Note that both background normal force values and the TMS-induced increments in those values scaled strongly with the external torque as illustrated in Figure 6. These relations could be described by second-order regressions with the coefficients of determination (computed over the data pooled over the subjects, loads, and trials) ranging from 0.9 to 0.99.

Similar to the normal force changes, the tangential forces changed during the early response to the TMS with background force. These changes were close to linear for the forces produced by the thumb, the middle finger, and the ring finger. They showed much less consistent changes for the index finger and the little finger. Linear relations between the background tangential force value and the magnitude of its TMS-induced response accounted, on average, for 74%, 11%, 98%, 85% and 26% of the total variance for the thumb, index, middle, ring and little fingers, respectively. The grand averages of the background tangential force and the TMS-induced change of tangential force across all subjects and loads are illustrated in Figure 7 as functions of the external torque. Note the high coefficients of determination for the thumb, the middle finger, and the ring finger (ranging from 0.87 to 0.99, panels A and C). Note also the strong linear scaling of the index finger force with external torque and the absence of such a scaling in the TMS-induced force increments (panel B).

Changes in the background moment of force and in the TMS-induced change in the total moment of force with external torque are shown in the top panel of Figure 8. The grand average of the moment of force showed a strong linear relation with external torque. The magnitude of the TMS-induced changes showed a non-linear scaling with external torque illustrated in Figure 8 with a second-order regression line (the coefficient of determination 0.99). Note the predominance of negative (supination) responses to the TMS.

Repeated-measures ANOVA showed that ΔM^n , ΔM^t and ΔM^{tot} were each affected by *Torque* significantly ($p < 0.001$), but not influenced by *Load* ($p > 0.2$) without a *Torque*×*Load* interaction ($p > 0.9$). Paired t-tests with Bonferroni corrections have confirmed that ΔM^{tot} tended to supinate the handle more in trials with supination efforts, while during pronation effort conditions the TMS could lead to supination or pronation ΔM^{tot} (Table 2).

Restoration of the equilibrium

The grand averages of the synergy restoration times are presented in Table 3. Recall that we characterized the process of synergy restoration using two time indices, the time of crude synergy restoration (Stage-1) and the time of achieving steady-state (Stage-2). The synergy restoration times for the normal forces, tangential forces, and moments of force did not depend on factors *Load* and *Torque*, as confirmed by two-way repeated-measures ANOVAs.

There were differences in the synergy restoration times for the normal forces, tangential forces, and moments of force. For Stage-1, the longest restoration time was seen for the total moment of force (357 ± 68 ms), followed by approximately similar restoration times for the normal forces (301 ± 47 ms) and the tangential forces (296 ± 30 ms). A two-way ANOVA using *Condition* as a factor (21 levels corresponding to all the external load-torque combinations) confirmed a significant difference between the times for M^{tot} and f^n ($p < 0.001$), but not between the times for f^n and f^t ($p > 0.5$).

During Stage-2, the sequence was different. The tangential forces reached steady-state first (in 1181 ± 168 ms), while the restoration of the normal forces and moments of force occurred approximately 300 ms later (1517 ± 201 ms and 1496 ± 160 ms, respectively). A two-way ANOVA using *Condition* as a factor showed the significant difference of the timing of Stage-2 between the times for f^t and f^n ($p < 0.001$), but not between the times for f^n and M^{tot} ($p > 0.5$).

Discussion

The main hypotheses formulated in the Introduction have been supported. In particular, the early responses of mechanical variables to TMS scaled nearly proportionally with the background values of those variables. These results corroborate earlier observations of a close to proportional increase in finger force response to TMS with an increase in the background finger force up to about 50% of the maximal voluntary contraction force (Danion et al. 2003). Our data show that this rule is true not only for normal finger forces but also for tangential forces produced by some of the digits, and for the total moment of force.

After the TMS-induced perturbation, all mechanical variables ultimately returned to values close to those prior to the TMS. However, the time profiles of the restoration processes could differ among the variables. In addition, restoration of synergic relations between pairs of variables at the thumb-VF level in Equations (1) typically happened before the variables themselves returned to new steady-state levels. Further discussion addresses implications of these findings for the control of multi-digit prehension.

Destructive TMS effects on the prehension synergy

Note that our analysis addressed changes in the mechanical variables produced by the digits on the handle, not muscle activations that might be responsible for these changes. As a result, we cannot address such issues as the relative role of TMS-induced responses in distal and proximal muscle groups. We will, however, address the issue of passive vs. active generation of tangential finger forces during the TMS-induced responses in a later subsection.

The prehension synergy was reflected at steady-state prior to TMS as co-varied changes in the elemental variables at the thumb-VF level (the variables in the left-hand sides of the equations of statics - see the Introduction). These observations are similar to earlier reports (Santello and Soechting 2000; Shim et al. 2003, 2005; reviewed in Zatsiorsky and Latash 2004, 2008). The three constituents of the prehension synergy were also obvious at the post-stimulation steady-state. However, there were transient violations of the synergy by the TMS. Such violations were particularly pronounced in the synergy constituents related to the production of the required tangential force and moment of force values. These observations argue against a recent suggestion that TMS does not disrupt the basic “architecture of motor plans” based on the analysis of the mechanical and muscle responses to TMS during static and dynamic contractions (Cros et al. 2007; see Introduction for more detail).

The mentioned law of proportional increase in the background force produced by TMS allows expecting proportional increase in the components of the overall hand action on the handle (see also Danion et al. 2003). The grip component of the prehension synergy requires positive co-variation of the normal forces of the thumb and VF (equation (2) in the Methods). Such co-varied changes could be expected after a TMS, based on the mentioned rule, and indeed were observed (see Figures 2A and 6).

In contrast, the synergy constituent related to the tangential force production requires negative co-variation of elemental variables (equation (3) in the Methods). The law of proportional force increase acts against the required negative co-variation and thus led to TMS-induced changes that violated that synergy constituent (see Figures 2B). Indeed, TMS tended to induce positively co-varying changes in the tangential forces produced by the thumb and VF thus destabilizing the total tangential force.

Although the overall finger force response to TMS scaled with force magnitude, individual fingers showed different correlation coefficients of the relations between the TMS-induced force changes and background force values. These relations for the normal force were

considerably weaker for the middle finger, while for the tangential force they were considerably weaker for the index and little fingers. One may tentatively suggest that these differences are related to the different involvement of the fingers in the production of the total tangential force and total moment of force. Note that an earlier study (Zatsiorsky et al. 2002) has suggested that the M and R fingers may be viewed as primarily load-supporting (their forces scale closely with external load) while the I and L fingers play a major role in maintaining the rotational equilibrium (their forces scale closely with external torque). Assume that the neural controller has an ability to modify sensitivity to TMS of neural structures responsible for force production by different digits. This assumption is supported by a study of the effects of practice on TMS-induced force responses in the task of multi-finger accurate force production (Latash et al. 2003). Under this assumption, neural structures controlling the load-supporting fingers may be expected to be tuned for the production of requisite tangential forces and show scaling of the TMS-induced responses with those forces. In contrast, structures controlling the torque-producing fingers may be expected to be tuned for the production of specific normal forces to ensure appropriate location of the point of VF normal force application - a major contributor to the total moment of force (Zatsiorsky et al. 2002). As such, they may be expected to show scaling of the TMS-induced responses with the magnitude of those forces.

Earlier studies of similar static prehensile tasks have shown that all four fingers produce normal forces in the same direction against the thumb force direction (fingers can only push, not pull), while the individual moments of force could be in opposite directions for some of the fingers and in some external loading conditions (Zatsiorsky et al. 2002, 2003). As a result, one cannot make similarly straight-forward predictions for the third synergy constituent related to rotational equilibrium (equation (4) in the Methods). Indeed, even the earliest TMS-induced changes in M^n and M^t were much less predictable and did not show positive co-variation (Figures 2C). Nevertheless, the TMS-induced changes in the total moment of force produced by the digits were proportional to the background magnitude of the moment of force (Figure 8), although the $\Delta M^{tot}(M^{tot})$ relation was skewed towards supination responses. This finding is compatible with an earlier report of higher voluntary torques produced into supination (clockwise) as compared to pronation (counterclockwise) during maximal torque production tasks performed while gripping a circular object (Shim et al. 2007). The finding could also get contribution from different patterns of agonist-antagonist activation during supination and pronation tasks. Note that the total moment of force is a variable that describes the combined action of many digits and muscles thus complicating interpretation of the skewed $\Delta M^{tot}(M^{tot})$ relation. We do not have a neurophysiological explanation for this finding and suspect that peculiarities of the cortical representations of different hand muscles and the orientation of the coil could lead to these results.

Taken together, the observations of the earliest responses to TMS suggest that these responses did not reflect synergic requirements imposed by the task but mostly followed the mentioned simple rule: A response in an elemental mechanical variable was proportional to its background magnitude.

Neurophysiological mechanisms of the prehension synergy are all but unknown. The mentioned destructive effects of TMS over the primary cortical motor area suggest that structures responsible for the co-varying changes in digit forces are either upstream of the stimulation site or involve the stimulation site (cf. Bonnard et al. 2007), but unlikely to be targets of neurons subjected to the TMS in our experiments. The TMS used in the study was likely to induce activation of corticospinal neurons both directly and trans-synaptically. If the site of synergy formation were downstream of the stimulation site (M1), the TMS would only change the input into that site, and synergic relations between elemental variables satisfying the equations (2)-(4) could be expected to persist.

Restoration of the prehension synergy

The prehension synergy took time to restore after a single TMS pulse. It should be noted, however, that patterns of co-variation between pairs of elemental variables corresponding to the equations of statics restored first (Stage-1), followed by continuing changes in the magnitude of the variables at the VF-thumb level. These observations support the idea of synergies as conjoint changes in elemental variables (Zatsiorsky and Latash 2004) by showing that synergies stabilizing a certain mechanical variable exerted on the hand-held object may be present while there are still ongoing changes in the magnitude of the contributing elemental variables (see also Latash et al. 2002; Zhang et al. 2006).

Another finding that supports the idea of restoration of synergy components independently of the magnitudes of the mechanical variables exerted on the handle is the fact that the timing of synergy restoration was not affected by manipulations of the external load and torque. In contrast, the magnitudes of the mechanical variables such as F_{GRIP} , F_{LOAD} , and M^{tot} were all affected by these factors as required by the equilibrium constraints.

The relative timing of the restoration of synergy components differed among the three variables, F_{GRIP} , F_{LOAD} , and M^{tot} . Co-variation of variables at the thumb-VF level related to F_{GRIP} and F_{LOAD} production was restored faster than co-variation of variables related to M^{tot} production. This result supports the idea of independent control of the total force and moment of force as required by the principle of superposition (Arimoto et al. 2001; Zatsiorsky et al. 2005). In contrast, it took longer for the magnitude of F_{GRIP} to come close to the new steady-state as compared to the magnitude of F_{LOAD} . The latter finding may be due to the fact that the production of a precise F_{LOAD} is necessary to keep the object steady in space, while over-gripping the object does not visibly violate the equilibrium as long as the normal forces of the thumb and VF are equal in magnitude.

Note that F_{GRIP} at a steady-state after TMS tended to be higher than prior to TMS. Several factors might have contributed to this phenomenon. First, agonist-antagonist co-contraction after a quick movement is known to be elevated for some time (Corcos et al. 1989). Second, an increase in F_{GRIP} has been reported following a transient perturbation to the hand-held object (Shim et al. 2006). Third, this phenomenon may represent a “stiffening strategy” (Johansson and Westling 1988) to mitigate kinematic effects of any perturbation.

Active production of the load-resisting force

Tangential forces in static tasks involving the vertical holding of an object in a prismatic grasp may be viewed as resulting from two major sources (Pataky et al. 2004). First, given a sufficient grip force, the hand-object interaction produces load-resisting, tangential forces passively, due to the deformation of the fingertips and possibly finger joints (Rumman 1991). Second, adjustments in tangential forces can result from neural signals generated by the central nervous system (supported by Rearick and Santello 2002).

A recent study of isometric voluntary finger force production in the radial-ulnar deviation has shown complex relations between purposefully produced forces and forces produced by non-instructed fingers (Pataky et al. 2007). The muscular apparatus involved in radial-ulnar finger deviation (tangential force production) involves primarily digit-specific intrinsic muscles. Hence, any interactions among the forces produced by individual digits in isometric conditions are likely to be of a central, neural origin. The synergic relations among the tangential forces produced by individual fingers (Shim et al. 2003, 2004) provide support for the neural hypothesis on the origin of the tangential forces in prehension.

Our observations also support this hypothesis. First, if the tangential forces were passive consequences of the mechanical hand-object interactions, TMS would not be expected to lead

to a consistent increase in those forces. However, in our experiments, not only TMS produced an increase in the tangential forces, but this increase scaled with the background level of the tangential forces, at least for some of the digits. This observation points at a neural origin of these forces. Indeed, an increase in the TMS-induced response is likely to reflect an increase in the excitability of neuronal pools (cortical or segmental) involved in the response that parallels an increase in the pool activation level (reviewed in Ellaway et al. 1999).

Acknowledgments

The study was in part supported by NIH grants AG-018751, NS-035032, and AR-048563.

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*. Springer Verlag; Berlin: 1985. p. 111-129.
- Arimoto S, Tahara K, Yamaguchi M, Nguyen PTA, Han HY. Principles of superposition for controlling pinch motions by means of robot fingers with soft tips. *Robotica* 2001;19:21–28.
- Baud-Bovy, G.; Rossi, S.; Prattichizzo, D. Effects of transcranial magnetic stimulation of the primary motor cortex on the grip and net forces in the tripod grasp; *Proc World Haptics Conference*; Pisa, Italy. 2005; p. 120-125.
- Baud-Bovy G, Prattichizzo D, Rossi S. Contact forces evoked by transcranial magnetic stimulation of the motor cortex in a multi-finger grasp. *Brain Res Bull* 2008;75:723–736. [PubMed: 18394518]
- Berardelli A, Inghilleri M, Polidori L, Priori A, Mercuri B, Manfredi M. Effects of transcranial magnetic stimulation on single and sequential arm movements. *Exp Brain Res* 1994;98:501–506. [PubMed: 8056070]
- Bonnard M, Galla C, De Graaf JB, Pailhous J. Corticospinal control of the thumb-index grip depends on precision of force control: a transcranial magnetic stimulation and functional magnetic resonance imagery study in humans. *Eur J Neurosci* 2007;25:872–880. [PubMed: 17328782]
- Classen J, Liepert J, Wise SP, Hallett M, Cohen LG. Rapid plasticity of human cortical movement representation induced by practice. *J Neurophysiol* 1998;79:1117–1123. [PubMed: 9463469]
- Corcos DM, Gottlieb GL, Agarwal GC. Organizing principles for single joint movements. II. A speed-sensitive strategy. *J Neurophysiol* 1989;62:358–368. [PubMed: 2769335]
- Cros D, Soto O, Chiappa KH. Transcranial magnetic stimulation during voluntary action: directional facilitation of outputs and relationships to force generation. *Brain Res* 2007;1185:103–116. [PubMed: 17961516]
- Danion F, Latash ML, Li S. Finger interactions studied with transcranial magnetic stimulation during multi-finger force production tasks. *Clin Neurophysiol* 2003;114:1445–1455. [PubMed: 12888027]
- Day BL, Rothwell JC, Thompson PD, Maertens de Noordhout A, Nakashima K, Shannon K, Marsden CD. Delay in the execution of voluntary movement by electrical or magnetic brain stimulation in intact man. *Brain* 1989;112:649–663. [PubMed: 2731025]
- Ellaway, PH.; Davey, NJ.; Ljubisavljevic, M. Magnetic stimulation of the nervous system. In: Windhorst, U.; Johansson, H., editors. *Modern Techniques in Neuroscience Research*. Springer Verlag; Berlin: 1999. p. 869-892.
- Gao F, Latash ML, Zatsiorsky VM. Internal forces during object manipulation. *Exp Brain Res* 2005;165:69–83. [PubMed: 15912369]
- Gao F, Latash ML, Zatsiorsky VM. Maintaining rotational equilibrium during object manipulation: Linear behavior of a highly non-linear system. *Exp Brain Res* 2006;169:519–531. [PubMed: 16328302]
- Johansson RS, Westling G. Programmed and triggered actions to rapid load changes during precision grip. *Exp Brain Res* 1988;71:72–86. [PubMed: 3416959]
- Kerr JR, Roth B. Analysis of multifingered hands. *J Robot Res* 1986;4:3–17.

- Latash ML, Yarrow K, Rothwell JC. Changes in finger coordination and responses to single pulse TMS of motor cortex during practice of a multi-finger force production task. *Exp Brain Res* 2003;151:60–71. [PubMed: 12740728]
- Latash ML, Scholz JF, Danion F, Schöner G. Finger coordination during discrete and oscillatory force production tasks. *Exp Brain Res* 2002;146:412–432.
- Latash ML, Scholz JP, Schöner G. Toward a new theory of motor synergies. *Motor Control* 2007;11:275–307.
- Lim CL, Yiannikas C. Motor evoked potentials: a new method of controlled facilitation using quantitative surface EMG. *Electroencephalog Clin Neurophysiol* 1992;85:38–41.
- MacKenzie, CL.; Iberall, T. The grasping hand. North-Holland; Amsterdam: 1994. 1994
- Pascual-Leone A, Dang N, Cohen LG, Brasil-Neto JP, Cammarota A, Hallett M. Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *J Neurophysiol* 1995;74:1037–1045. [PubMed: 7500130]
- Pataky TC, Latash ML, Zatsiorsky VM. Tangential load sharing among fingers during prehension. *Ergonomics* 2004;47:876–889. [PubMed: 15204280]
- Pataky TC, Latash ML, Zatsiorsky VM. Finger interaction during maximal radial and ulnar deviation efforts: Experimental data and linear neural network modeling. *Exp Brain Res* 2007;179:301–312. [PubMed: 17334750]
- Ravnborg M, Blinkenberg M, Dahl K. Standardization of facilitation of compound muscle action potentials evoked by magnetic stimulation of the cortex. *Electroencephalog Clin Neurophysiol* 1991;81:195–201.
- Rearick MP, Santello M. Force synergies for multifingered grasping: effect of predictability in object center of mass and handedness. *Exp Brain Res* 2002;144:38–49. [PubMed: 11976758]
- Rumman, WS. Statically indeterminate structures. Wiley-Interscience; New York: 1991.
- Santello M, Soechting JF. Force synergies for multifingered grasping. *Exp Brain Res* 2000;133:457–467. [PubMed: 10985681]
- Savescu AV, Latash ML, Zatsiorsky VM. A technique to determine friction at the fingertips. *J Appl Biomech* 2008;24:43–50. [PubMed: 18309182]
- Shim JK, Huang J, Latash ML, Zatsiorsky VM. Multi-digit maximal voluntary torque production on a circular object. *Ergonomics* 2007;50:660–675. [PubMed: 17454086]
- Shim JK, Latash ML, Zatsiorsky VM. Prehension synergies: trial-to-trial variability and hierarchical organization of stable performance. *Exp Brain Res* 2003;152:173–184. [PubMed: 12898101]
- Shim JK, Latash ML, Zatsiorsky VM. Finger coordination during moment production on a mechanically fixed object. *Exp Brain Res* 2004;157:457–467. [PubMed: 15024540]
- Shim JK, Latash ML, Zatsiorsky VM. Prehension synergies: trial-to-trial variability and principle of superposition during static prehension in three dimensions. *J Neurophysiol* 2005;93:3649–3658. [PubMed: 15728759]
- 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]
- Ugawa Y, Terao Y, Hanajima R, Sakai K, Kanazawa I. Facilitatory effect of tonic voluntary contraction on responses to motor cortex stimulation. *Electroencephalog Clin Neurophysiol* 1995;97:451–454. [PubMed: 8536598]
- Van der Kamp W, VanDenBrink AM, Zwinderman AH, Kramer CGS, van Dijk JG. Differential effects of unilateral magnetic cortical stimulation on reaction time. *Electromyogr Clin Neurophysiol* 1998;38:59–64. [PubMed: 9532435]
- Yoshikawa T, Nagai K. Manipulating and grasping forces in manipulation by multifingered robot hands. *IEEE Trans Robot Automat* 1991;7:67–77.
- Zatsiorsky VM, Gregory RW, Latash ML. Force and torque production in static multifinger prehension: biomechanics and control. I. Biomechanics. *Biol Cybern* 2002;87:50–57. [PubMed: 12111268]
- Zatsiorsky VM, Latash ML. Prehension synergies. *Exerc Sport Sci Rev* 2004;32:75–80. [PubMed: 15064652]
- Zatsiorsky VM, Latash ML. Multi-finger prehension: An overview. *J Mot Behav*. 2008in press

- Zatsiorsky VM, Latash ML, Gao F, Shim JK. The principle of superposition in human prehension. *Robotica* 2004;22:231–234.
- Zatsiorsky VM, Gao F, Latash ML. Prehension synergies: Effects of object geometry and prescribed torques. *Exp Brain Res* 2003;148:77–87. [PubMed: 12478398]
- Zhang W, Zatsiorsky VM, Latash ML. Accurate production of time-varying patterns of the moment of force in multi-finger tasks. *Exp Brain Res* 2006;175:68–82. [PubMed: 16779549]

Figure 1.

Schematic drawing of the apparatus with five sensors mounted on the handle with the T-shaped attachment. The openings along the horizontal bar represent the different locations of the load attachment (D) to achieve the target external torques. The right panels show the sensor-centered reference frame, the sensor cap and the definition of the point of force application. The figure is not drawn to the scale.

Figure 2.

The relations between the VF and thumb normal forces (panel A), tangential forces (panel B), and moments produced by the normal forces and by the tangential forces (panel C) before and after a TMS stimulus. A representative example from a typical subject. Red dots: variations prior to the TMS. T=0 is the time when TMS was applied. T_p is the time of normal force to reach peak force magnitude after TMS. Green dots: the changes immediately following the TMS. Blue dots: the first stage of the synergy restoration period (between times T1 and T2). Black dots: the second stage of synergy restoration (after T2). The slanted dashed lines are the equality lines corresponding to the equations of statics.

Figure 3.

A: Time series of the sum of normal forces produced by the four fingers and the EMG profiles of the FDS and EDC (arbitrary units; the EDC EMG is inverted for better visualization). B: The distance from the data points to the equality line, $\text{Dist}(t)$, and its standard deviation $\text{SD}(t)$. T1 and T2 indicate the beginning of Stage-1 and Stage-2 of the normal force synergy restoration.

Figure 4.

A typical example of the time series of normal forces (A), tangential forces (B), total normal force and total tangential force (C), and total moment of force (D) following a TMS that occurred at time zero. A representative example for a typical subject holding a load of 0.75 kg with the external torque of -0.4 Nm.

Figure 5.

The percentage of trials with negative changes in the moment of force, ΔM^n (stars), ΔM^t (open squares) and ΔM^{tot} (filled circles) for each external torque. Negative changes signify an increase in the supination effort or a decrease in the pronation effort. Averaged across subjects data are presented.

Analysis of Normal Forces

Figure 6.

The background values of the normal digit forces (BG, filled symbols) and the TMS-induced changes in the normal digit forces (TMS, open symbols) as functions of the external torque with second-order regression lines and coefficients of determination. Averaged across subjects data are shown for the thumb (A), index and little fingers (B), and ring and middle fingers (C). Note the similar shapes of the two dependences.

Analysis of Tangential Forces

Figure 7.

The background values of the tangential digit forces (BG, filled symbols) and the TMS-induced changes in the tangential digit forces (TMS, open symbols) as functions of the external torque with linear regression lines and coefficients of determination (interpolations are shown for irregular patterns). Averaged across subjects data are shown for the thumb (A), index and little fingers (B), and ring and middle fingers (C). Note the similar shapes of the two dependences in panels A and C but not in panel B.

Analysis of Moments of Force

Figure 8.

TMS-induced changes in the total moment of force (Moment-TMS, solid second-order regression line) and the background total moment of force (Moment-BG, dashed linear regression line) as functions of the external torque. Note the non-linear change in the TMS-induced changes with the predominance of supination (negative) responses. Averaged across subjects data are shown with coefficients of determination.

Table 1

TMS-induced changes in tangential forces

External torque, Nm	Supination efforts			Zero	Pronation efforts		
	0.6	0.4	0.2		-0.2	-0.4	-0.6
Δf_{th}^t , N	3.48±0.80	2.66±0.63	2.45±0.57	1.89±0.54	1.79±0.56	1.69±0.56	1.61±0.54
% of positive Δf_{vf}^t occurrences	40.1	64.8	74.1	81.5	87.0	85.2	90.7
Δf_{vf}^t , N	0.06±0.32	0.52±0.39	0.65±0.35	0.94±0.34	1.15±0.38	1.18±0.34	1.34±0.37
Δf_{total}^t , N	3.42±0.65	3.17±0.48	3.10±0.45	2.83±0.46	2.94±0.42	2.87±0.50	2.95±0.44

The data are shown for different external torques that required supination or pronation efforts, Δf_{th}^t , Δf_{vf}^t , and Δf_{total}^t stand for the TMS-induced changes in the tangential forces of the thumb, virtual finger, and the total tangential force. Averages across subjects with standard errors are presented.

Table 2

TMS-induced changes in the moment of force

	Supination effort			0	Pronation effort		
	0.6	0.4	0.2		-0.2	-0.4	-0.6
External torque, Nm							
ΔM^u , Nmm	-194±36	-129±32	-80±19	-11±11	9±15	25±28	50±29
ΔM^l , Nmm	-127±37	-77±33	-65±30	-34±28	-23±31	-18±28	-10±29
ΔM^{tot} , Nmm	-321±64	-206±50	-144±34	-46±28	-14±34	7±35	41±43

The data are shown for different external torques that required supination or pronation efforts. ΔM^u , ΔM^l , ΔM^{tot} stand for the changes in the moment of normal force, moment of tangential force and total moment of force. Averages across subjects with standard errors are presented.

Table 3

Timing of synergy restoration

		Total normal force	Total tangential force	Total moment of force
Stage-1 (T1)	Mean	301	296	357
	Standard error	47	30	68
Stage-2 (T2)	Mean	1517	1181	1496
	Standard error	201	168	160

The times of the initiation of the two stages of synergy restoration (in ms) are presented for the three characteristics of the hand mechanical action (means across the subjects and standard errors.)