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Hierarchies of synergies: an example of two-hand, multi-finger tasks

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Abstract

We explored the ability of the central nervous system (CNS) to assemble synergies stabilizing the output of sets of effectors at two levels of a control hierarchy. Specifically, we asked a question: can the CNS organize both two-hand and within-a-hand force stabilizing synergies in a simple two-hand force production task that involves two fingers per hand? Intuitively, one could expect a positive answer; that is, forces produced by each hand are expected to co-vary negatively across trials to bring down the total force variability, while forces produced by each finger within-a-hand are expected to co-vary negatively to reduce the variability of that hand's contribution to the total force. The subjects were instructed to follow a trapezoidal time profile with the signal corresponding to the force produced by a set of instructed fingers in one-hand tasks with two-finger force production and in two-hand tasks with involvement of both symmetrical and asymmetrical finger pairs in the two hands. Finger force co-variation across trials was quantified and used as an index of stabilization of the force produced by all the instructed fingers, and of the force produced by finger pairs within-a-hand. No major differences were seen between the dominant and the non-dominant hand and between the two-hand tasks with symmetrical and asymmetrical finger involvement. Stronger synergies were seen in the index–middle finger pair as compared to the ring–little finger pair. The main result of the study is the significantly weaker or even lacking two-finger force stabilizing synergies within-a-hand during two-hand tasks while such synergies were present in one-hand tasks. This observation points at a potential limitation in the ability of the CNS to organize synergies at two levels of a control hierarchy simultaneously. It also allows suggesting a hypothesis on two types of synergies in the human motor repertoire, well-practiced synergies that form a library serving as the foundation for all novel actions, and freshly assembled synergies.

Keywords

Hand; Synergy; Finger; Force production; Bilateral action

Introduction

When a person tries to produce a certain level of force or a certain time profile of force with several fingers pressing together in parallel, the variability of the total force across repetitive trials is typically smaller than what one could expect based on the magnitudes of variability of individual finger forces (Li et al. 1998; Scholz et al. 2002; Shim et al. 2003a; Shinohara et al. 2003). This observation suggests that commands to individual fingers do not vary independently across trials but rather they are organized by the central nervous system (CNS) into a synergy with the purpose to minimize deviations of the total force from its desired value or from a time series of values. We consider synergies as neural organizations that produce

stable output variables by coordinated action of several elements of a system. Several recent studies quantified force-stabilizing synergies within a range of pressing and prehensile tasks (Kang et al. 2004; Latash et al. 2001, 2004; Li et al. 1998; Santello and Soechting 2000; Scholz et al. 2003; Shim et al. 2003a, b, 2005).

When two hands cooperate to produce a desired common motor effect, actions by each hand have also been shown to form synergies stabilizing the common output (Kang et al. 2004; Paulignan et al. 1989; Scholz and Latash 1998). In particular, changing the force produced by a hand on the bottom of an object grasped by the other hand is accompanied by simultaneous adjustments in the grasping force (Scholz and Latash 1998).

The notion of hierarchical control of natural movements has been invoked by many researchers (Bernstein 1967; Arbib et al. 1985). In particular, prehensile actions by the hand have commonly been viewed as produced by a control hierarchy involving at least two steps. First, the task is distributed between the thumb and a virtual finger [VF, an imagined finger that produces a mechanical action equivalent to that of the actual fingers of the hand (Arbib et al. 1985; MacKenzie and Iberall 1994)]. Second, action by the VF is distributed among the actual fingers. Along similar lines, control of a two-hand action may be viewed as involving two steps: (1) distributing the task between the two hands; and (2) distributing actions by each hand among its digits. At each level, one may expect a synergy stabilizing the combined action of the elements (the two hands at the first step and the individual fingers at the second step) according to the input from a hierarchically higher level (the task for the first step, and required hand action for the second step).

There have been only a couple of studies trying to address issues of possible interference between within-a-hand and two-hand synergies (Kang et al. 2004; Li et al. 2002). In particular, Li et al. (2002) showed strong interference effects between hand actions when a one-hand multi-finger action turned into a two-hand action. Kang et al. (2004) purposefully used a very unusual multi-finger task to study learning of multi-finger synergies. The study described no within-a-hand synergies to stabilize the total force produced by each hand prior to practice. Such synergies emerged after three days of practice.

Given that within-a-hand and two-hand synergies have been documented, one could formulate the following question: can the CNS organize both two-hand and within-a-hand force stabilizing synergies in a simple two-hand force production task that involves two fingers per hand? Intuitively, one could expect a positive answer; that is forces produced by each hand are expected to co-vary negatively across trials to bring down the total force variability, while forces produced by each finger within-a-hand are expected to co-vary negatively to reduce the variability of that hand's contribution to the total force.

However, it is possible that the task of creating two synergies at two hierarchically different levels at the same time may not be trivial for the controller. Is this an easy task for the CNS? We do not know. Thus, an alternative hypothesis is that the CNS may be unable to create synergies at the two hierarchical levels. If this is true, we expect to see two-hand synergies stabilizing the total force time profile in the absence of within-a-hand synergies that would stabilize each hand's contribution to the task. Such results would contrast force stabilizing synergies reported for one-hand tasks (Latash et al. 2001, 2002a, Latash et al. b; Scholz et al. 2002).

To test the two hypotheses, we performed a study of multi-finger production of an accurate time profile of the total force with a set of fingers pressing in parallel. The instructed finger groups involved two or four fingers, as well as one or two hands. We expected to see predominantly negative co-variation among finger forces in one-hand tasks; that is force stabilizing synergies (Latash et al. 2001, 2002a, Latash et al. b; Scholz et al. 2002). In two-

hand tasks, we expected to see force-stabilizing synergies when each hand is viewed as a force generator (Kang et al. 2004). However, we did not know a priori whether pairs of fingers within each hand would be united into a synergy stabilizing the total force produced by this hand.

The design of the study also allowed us to compare force stabilizing synergies between the dominant hand and non-dominant hand, between the index + middle (IM) and ring + little (RL) finger pairs, and between symmetrical (IM + IM and RL + RL) and asymmetrical (IM + RL and RL + IM) two-hand tasks. No a priori hypotheses could be formulated with respect to these comparisons. However, differences could be expected based on earlier studies that have shown effects of hand dominance on indices of finger interaction (Li et al. 2000), different ability to control finger forces independently across fingers (typically, the index finger is better controlled individually as compared to the other fingers (Li et al. 1998; Zatsiorsky et al. 1998, 2000), and differences in bilateral effects in symmetrical and asymmetrical two-hand tasks (Li et al. 2002). Most of the cited studies used maximal force production tasks; thus one cannot readily make predictions with respect to our task of accurate sub-maximal force production.

To summarize, the main specific question asked in the study was: can the CNS organize both two-hand and within-a-hand force stabilizing synergies in a simple two-hand force production task that involves two fingers per hand?

Methods

Participants

Eight (four males and four females) university students served as subjects in this study. Average anthropomorphic data for the male subjects were: 27 ± 2 years of age, 1.79 ± 0.06 m in height, 85.0 ± 16.0 kg in mass, 20.0 ± 0.9 cm for right hand length, 8.8 ± 0.3 cm for right hand width, 20.2 ± 0.7 cm for left hand length, and 8.9 ± 0.4 cm for left hand width. Average anthropomorphic data for the female subjects were: 26 ± 4 years of age, 1.63 ± 0.03 m in height, 59.5 ± 5.9 kg in mass, 17.5 ± 0.8 cm for right hand length, 7.8 ± 0.3 cm for right hand width, 17.8 ± 0.7 cm for left hand length, and 7.8 ± 0.2 cm for left hand width. Hand length was measured as the distance from the tip of the distal phalanx of digit three to the distal crease of the wrist with the hand in a neutral flexion/extension pose. Hand width was measured between the lateral aspects of the index and little finger meta-carpophalangeal (MCP) joints. All subjects were right-handed according to their preferential use of the hand during daily activities such as writing, drawing, and eating. The subjects had no previous history of neuropathies or traumas to the upper limbs. None of the subjects had a history of long-term involvement in hand or finger activities such as typing and playing musical instruments. All subjects gave informed consent according to the procedures approved by the Office of Regulatory Compliance of the Pennsylvania State University.

Experimental setup

Eight unidirectional piezoelectric force sensors (model 208AO3; PCB Piezotronic Inc., Depew, NY, USA), were used to measure forces produced by the individual fingers of both hands. Each sensor was covered with a cotton pad to increase friction and prevent the influence of finger skin temperature on the force measurements. Two groups of four force sensors were placed within aluminum frames ($140 \text{ mm} \times 90 \text{ mm}$ each) in a groove on a wooden board. The two frames were spaced 40 cm apart. The sensors were medio-laterally spaced 30 mm apart from each other within the aluminum frames. The position of the sensors in the sagittal plane could be adjusted within 60 mm in order to fit individual subject hand anatomy (see Fig. 1).

During the experiment, the subject sat in a chair facing the testing table with his/her upper arms at approximately 45° of abduction in the frontal plane and 45° of flexion in the sagittal plane, and the elbow at approximately 45° of flexion (Fig. 1). The forearms rested on the wooden board that contained the sensors. The forearms were secured to the board via two sets of Velcro straps. The midline of the board was aligned with the midline of the participant's body, and the positions of the hands were symmetrical with respect to the midline of the body. A custom-fit support object was placed underneath each of the participant's palms to help maintain a constant configuration of the hand and fingers. The MCP joints were approximately 20° in flexion and all interphalangeal joints were slightly flexed such that each hand formed a dome. Subjects were permitted to select comfortable positions of the thumbs during the experiment. A computer monitor was located 0.65 m away from the subject. The monitor displayed the task (described in the next section). Force data were sampled at 1,000 Hz.

Procedure

The experiment consisted of a few control trials and a main set of tasks. In the control trials, the subjects were required to produce maximal voluntary contraction (MVC) forces by the pairs of fingers used in the main tasks. The pairs of fingers used were: IM_R , IM_L , RL_R , and RL_L ; where I = index, M = middle, R = ring, L = little, and the subscripts denote the hand to which the fingers belong (R = right, L = left). In these trials, the subjects were required to press with the instructed set of fingers "as hard as possible". Each MVC trial started with the subject seating quietly with the hands resting on the sensors. A sound signal was given and then a cursor showing the total force produced by the instructed fingers started to move over the screen. The subject was given a time interval of 3 s to reach maximal force by pressing with the instructed fingers. The subjects were told not to pay attention to possible force production by non-instructed fingers as long as the instructed fingers produced maximal force. There were intervals of at least 30 s between successive MVC trials. Two MVC trials per finger pair were collected and the trial with the highest peak force was selected for the subsequent tasks. The peak force value for each pair obtained in the MVC trials was used to set up the templates for the main task.

There was one main set of tasks that included ten conditions ($IM_R + RL_L$, $RL_R + IM_L$, $IM_R + IM_L$, $RL_R + RL_L$, $IMRL_R$, $IMRL_L$, IM_R , IM_L , RL_R , and RL_L). Prior to each trial the subject sat relaxed with the digits of each hand resting on the sensors. The computer generated two beeps (a "get ready" signal), and a cursor showing the total force produced by the instructed set of fingers started to move along the screen. The screen also showed the required total force profile (see Fig. 1) and the task was to follow the shown profile with the cursor. Each profile started with a background force of 5% of the MVC for the instructed set of fingers for 3 s. This was followed by an oblique line that led to 20% of the MVC over 1.5 s. The line at 20% MVC remained constant for 2 s, then it turned into another oblique line leading back to the 5% MVC level over 1.5 s. The 5% MVC line remained constant for the remaining 2 s of the trial (see Fig. 2). We used a trapezoidal time profile of the total force to test possible difference of the force stabilizing synergies during steady-state force production and during the production of ramp time profile of force. Such differences could be expected based on earlier studies (Shim et al. 2005b).

In each condition, subjects performed 15 trials with 8 s intervals between the trials. There were 3 min intervals between each 15-trial series. Overall, there were 150 experimental trials. Prior to each series, subjects were permitted to practice the conditions as many times as needed until they were comfortable with the tasks. On average, subjects performed two practice trials per task plus or minus one practice trial. The conditions were presented in a balanced order across subjects.

Data analysis

The data were processed offline using customized MATLAB software (Mathworks Inc., Natick, MA, USA). The force data from the main task were low-pass filtered at 10 Hz using a second order, zero-lag Butterworth filter. The following variables were computed at each point in time for each subject over the fifteen trials within each condition. Results of the computations formed the following time functions:

1. The average total force, $F_{TOT}(t)$ of explicitly involved task fingers, and its variance, $\text{Var}F_{TOT}(t)$;
2. The sum of variances of each individual finger force, $\sum \text{Var}F_i(t)$;
3. Variance of each hand's force across trials, $\text{Var}F_{\text{hand}}(t)$. Hand's force was computed as the sum of the forces produced by the explicitly involved fingers of that hand;
4. The sum of variances of finger forces within a hand, produced by the explicitly involved fingers of that hand, $\sum \text{Var}F_{i\text{-hand}}(t)$;
5. The difference between $\sum \text{Var}F_i(t)$ and $\text{Var}F_{TOT}(t)$: $\Delta V_{\text{all-fingers}}(t) = \sum \text{Var}F_i(t) - \text{Var}F_{TOT}(t)$;
6. The difference between the sum of $\text{Var}F_{\text{hand}}(t)$ across the two hands and $\text{Var}F_{TOT}$: $\Delta V_{\text{two-hand}}(t) = \sum \text{Var}F_{\text{hand}}(t) - \text{Var}F_{TOT}(t)$ (only for two-hand tasks); and
7. The difference between $\sum \text{Var}F_i(t)$ for finger forces within-a-hand and $\sum \text{Var}F_{\text{hand}}(t)$ computed for each hand separately: $\Delta V_{\text{within-a-hand}}(t) = \sum \text{Var}F_{i\text{-hand}}(t) - \sum \text{Var}F_{\text{hand}}(t)$.

All ΔV indices were normalized by the sum of variances of the forces produced by corresponding sets of effectors (fingers for $\Delta V_{\text{all-fingers}}$ and $\Delta V_{\text{within-a-hand}}$ and hands for $\Delta V_{\text{two-hand}}$) to allow for comparisons among different ΔV indices across conditions and subjects. Note that the ΔV indices have been defined in such a way that their positive values implied predominantly negative co-variation among forces produced by fingers (or hands); we interpret such values as signs of a force stabilizing synergy (cf. Kang et al. 2004; Shim et al. 2005). Larger positive ΔV values correspond to larger amounts of negative co-variation—a stronger synergy. $\Delta V = 0$ implies independent variation of finger (hand) forces—the absence of a synergy. Note that the described normalization limited the value of ΔV indices to +1 for a perfect force stabilizing synergy. Additionally, to study changes in ΔV indices, we used an index $\Delta\Delta V$ reflecting the maximum change in ΔV from a steady-state interval to a ramp interval. This analysis was done for intervals 1 and 2 (as $\Delta\Delta V_1$) and intervals 3 and 4 ($\Delta\Delta V_2$). This index was used to make the data comparable across subjects since each subject showed different baseline values of ΔV across the interval changes.

Indices of force and force synergies were analyzed within five segments of the template trapezoidal profile. For this purpose, these indices were averaged over time intervals of 0.5 s in the middle of the corresponding segments as illustrated in Fig. 2. The time intervals were: 2.20–2.70 s, 3.50–4.00 s, 5.25–5.75 s, 7.00–7.50 s, and 8.50–9.00 s. Note that the first and last time segments (and consequently time intervals) did not include the very beginning or end of each trial in order to avoid irregularities in force production near the beginning and end of trials.

In this study, we decided against using the analysis based on comparison of variances of hypothetical commands to fingers (finger modes, Latash et al. 2001; Scholz et al. 2002). To use this analysis, one has to know how small intentional changes in force produced by one finger affect forces produced by other fingers (so-called, enslaving matrices, Latash et al. 2001; Zatsiorsky et al. 2000). Obtaining such matrices for two-hand tasks has never been done

and would turn into an experiment of its own. Note, however, that ignoring enslaving (which contributes to positive co-variation of finger forces) can only lead to an underestimation of force stabilizing synergies (which benefit from negative co-variation of finger forces).

The averages of F_{TOT} , $\text{Var}F_{TOT}$, $\Delta V_{\text{all-fingers}}$, $\Delta V_{\text{within-a-hand}}$, and $\Delta V_{\text{two-hand}}$ were found during each segment of the trapezoid template of each condition for each subject, as described earlier. While individual trials were naturally aligned by the template pattern, the actual times of initiation of changes in the total force during the two ramp phases were defined as the times when the first derivative of the total force reached 5% of its peak level observed during the ramp-up and ramp-down phases, respectively, for each trial separately.

Different types of analysis of variance of ΔV indices were performed to address the following three basic questions:

1. Do finger forces within a hand co-vary to stabilize the average time profile of the total force produced by the hand? For this analysis, we computed $\Delta V_{\text{within-a-hand}}(t)$ as defined earlier and analyzed it within the five time intervals shown in Fig. 2.
2. Do forces generated by each hand co-vary to stabilize the average time profile of the total force? For this analysis, we used $\Delta V_{\text{two-hand}}(t)$.
3. Do forces generated by all the fingers involved in the task co-vary to stabilize the average time profile of the total force? For this analysis, we computed $\Delta V_{\text{all-fingers}}(t)$.

The purpose of further analysis was to answer five specific questions:

1. Are there differences in synergies between left and right hands?
2. Are there differences in synergies between finger pairs?
3. Do synergies in asymmetric tasks differ depending on the distribution of fingers?
4. Are there differences in synergies between symmetric and asymmetric tasks?
5. Are there differences between one-hand two-finger synergies and two-finger within-a-hand synergies in a two-hand task?

The next section is structured to address, first, the general patterns of performance, followed by analysis related to the first four questions, and then the last question is addressed.

Statistics

The data are presented in the text and figures as means and standard errors. Several repeated-measures analyses of variance (ANOVAs) were performed with the factors: *Interval* (five levels, one to five), *Task* (two levels, one for conditions in which the task fingers were distributed within one hand and another for conditions in which the task fingers were distributed over two hands), *hand* (two levels, right and left), *finger-pair* (two levels, IM and RL), *index* (three levels, $\Delta V_{\text{all-fingers}}$, $\Delta V_{\text{within-a-hand}}$, and $\Delta V_{\text{two-hand}}$), *condition* (ten levels, one for each condition/finger combination tested in the experiment; levels were selected depending on particular comparisons), and *symmetry* (two levels, one for conditions in which symmetric finger pairs in two-hand tasks were used and another in which asymmetric finger pairs in two-hand tasks were used). The data were checked for violations of sphericity across levels of a within-subject factor. We used the Huynh–Feldt criterion to reduce the degrees-of-freedom when necessary. Post hoc analyses of pairwise comparisons were performed using Bonferroni corrections when necessary.

Results

In this section, the results are presented in the following order. The first sub-section titled “General Force and Variance Time Profiles” describes the general characteristics of force output, variability of total force output ($\text{Var}F_{\text{TOT}}$), and $\Delta V_{\text{all-finger}}$ profiles with respect to the time intervals used in this study. The second sub-section titled “Effects of Hand, Finger Pair, and Symmetry” describes the differences between the right and left hands, between the IM and RL finger pairs, and between symmetrical and asymmetric tasks on both $\text{Var}F_{\text{TOT}}$ and ΔV indices. The final sub-section titled “Difference Between One- and Two-Hand Tasks” addresses the main hypothesis of the study. It describes the differences in both $\text{Var}F_{\text{TOT}}$ and ΔV profiles for finger pairs involved in one- and two-hand tasks.

General force and variance time profiles

During each of the conditions, the subjects were able to follow the template without obvious errors and large corrective actions. An example of typical performance by a representative subject is shown in Fig. 3. Total force time profiles as well as force profiles for finger pairs for the task $\text{IM}_R + \text{RL}_L$ are shown in panel A while total force and individual finger force time profiles are shown for the task IM_R in panel B.

Overall, each subject performed each task quite accurately during the three steady-state segments of the trapezoid (segments 1, 3, and 5). Deviations of the average performance from the template lines were of the order of the line thickness on the screen. Variability in the total force ($\text{Var}F_{\text{TOT}}$) increased during the ramp segments. This can be seen in Fig. 4, which shows time profiles of $\text{Var}F_{\text{TOT}}$ for a representative subject averaged across all one- and two-hand tasks.

$\text{Var}F_{\text{TOT}}$ is much lower during the steady-state intervals 1, 3, and 5 as compared to the ramp segments 2 and 4. This finding was consistent for both four-finger and two-finger tasks, as seen in Fig. 4.

A one-way ANOVA over the five intervals confirmed this finding. Overall, it was found that $\text{Var}F_{\text{TOT}}$ showed significant differences across the five intervals ($F_{[4, 395]} = 191.71$; $P < 0.001$). There were no differences among the steady-state intervals in $\text{Var}F_{\text{TOT}}$ values just as the two ramp intervals were similar to each other. However, the $\text{Var}F_{\text{TOT}}$ values for the steady-state intervals were significantly different than the ramp intervals: on average, ramp intervals exhibited more than five times the total force variance than steady-state intervals. This finding was confirmed via pairwise post hoc Tukey tests which revealed that $\text{Var}F_{\text{TOT}}$ values during intervals 1, 3, and 5 were different from those during intervals 2 and 4 at $P < 0.001$. Post hoc analysis did not reveal a difference among intervals 1, 3, and 5, $P > 0.05$.

To study co-variation among fingers forces, we used a normalized index $\Delta V_{\text{all-fingers}}$ computed in such a way that its positive values reflected predominantly negative co-variation among the finger forces (a force-stabilizing synergy, see Data analysis). Over all tasks and subjects, $\Delta V_{\text{all-fingers}}$ was positive and close to unity over the three steady-state segments. It showed a drop during the ramp segments. Figure 5 illustrates this general finding with the $\Delta V_{\text{all-fingers}}$ profiles generated by a typical subject in two conditions, $\text{IM}_R + \text{RL}_L$ and IM_R . A one-way ANOVA over the five intervals confirmed this finding. Overall, it was found that $\Delta V_{\text{all-fingers}}$ showed significant differences across the five intervals ($F_{[4, 395]} = 84.40$; $P < 0.001$). In general, the steady-state intervals exhibited higher $\Delta V_{\text{all-fingers}}$ values when compared to the ramp intervals. Pairwise post hoc Tukey tests revealed that ΔV values in intervals 1 and 5 were significantly different from the values in intervals 2 and 4 at $P < 0.001$. Post hoc analysis did not reveal differences between intervals 1 and 5 as well as intervals 2 and 4, $P > 0.05$.

Effects of hand, finger pair, and symmetry

In order to examine possible differences between the right and left hands, a subset of conditions were selected. The following conditions were used as right hand conditions: IM_R, RL_R, IMRL_R, and IM_R + RL_L. Similarly, the following conditions were used as left hand conditions: IM_L, RL_L, IMRL_L, and IM_L + RL_R. VarF_{TOT} and ΔV_{all-fingers} were averaged within each group of conditions and subjected to repeated-measures ANOVAs with the factors *Interval* and *Hand*. There was a main effect of *Interval* for both VarF_{TOT} ($F_{[1.748, 104.86]} = 112.557, P < 0.001$) and ΔV_{all-fingers} ($F_{[3.217, 193.003]} = 66.247, P < 0.001$) without a *Hand* effect or a significant interaction. For VarF_{TOT}, the steady-state intervals (1, 3, and 5) exhibited lower levels of variance as compared to the ramp intervals (2 and 4). Pairwise post hoc Tukey tests revealed that both indices during intervals 1, 3, and 5 were significantly different from their values in intervals 2 and 4 at $P < 0.001$. Post hoc analysis did not reveal differences between intervals 3 and 5 as well as intervals 2 and 4, $P > 0.05$. The low levels of VarF_{TOT} in the steady-state intervals corresponded to the ΔV_{all-fingers} values close to unity. The ΔV_{all-fingers} indices were highest in the steady-state intervals (1, 3, and 5) and lowest in the ramp intervals (2 and 4). Pairwise post hoc Tukey tests revealed that the values in intervals 1, 3, and 5 were significantly different from those in intervals 2 and 4 at $P < 0.001$. Post hoc analysis did not reveal differences between intervals 1 and 5 as well as intervals 2 and 4, $P > 0.05$.

In order to examine possible differences between the two finger pairs used in this experiment, two specific analyses were used. In the first, only conditions in which two fingers (single pairs) were used are considered (IM_R, IM_L, RL_R, and RL_L; data averaged across each of the conditions for each subject were used). In the second, finger pairs used in two-hand tasks were examined (IM_R + RL_L, IM_L + RL_R, IM_R + IM_L, and RL_R + RL_L; data averaged across each of the conditions for each subject were used). For both of the finger pair analyses, two-way repeated-measures ANOVAs with factors *Interval* and *Finger-Pair* were used to analyze both VarF_{TOT} and ΔV_{all-fingers} indices.

Across the one-hand tasks, only the main effect of *Interval* was found ($F_{[1.690, 23.657]} = 68.602, P < 0.001$) for VarF_{TOT} with no significant interactions. The steady-state intervals (1, 3, and 5) had the lowest values of VarF_{TOT} while the ramp intervals showed the highest values. Pairwise post hoc Tukey tests revealed that VarF_{TOT} during intervals 1, 3, and 5 was significantly different from its values in intervals 2 and 4 at $P < 0.001$. Post hoc analysis did not reveal differences between intervals 1 and 3 and 3 and 5 as well as intervals 2 and 4, $P > 0.05$. For the ΔV_{all-fingers} analysis, a main effect of *Interval* ($F_{[2.985, 41.794]} = 53.556, P < 0.001$) and a significant interaction *Interval* × *Finger-Pair* ($F_{[2.985, 41.794]} = 3.385, P < 0.05$) were found. In the steady-state intervals, ΔV_{all-fingers} was higher than in the ramp intervals. The interaction reflected the fact that during the ramp intervals, the ΔV_{all-fingers} index for the IM pair was less than for the RL pair, as seen in Fig. 6. However, in the steady-state intervals, the ΔV_{all-fingers} index for the IM pair was higher than for the RL pair. Pairwise post hoc Tukey tests revealed that ΔV values in intervals 1, 3, and 5 were significantly different from those in intervals 2 and 4 at $P < 0.001$. Post hoc analysis did not reveal differences between intervals 1 and 3 and 1 and 5 as well as intervals 2 and 4, $P > 0.05$.

In the two-hand tasks, only a main effect of *Interval* was found ($F_{[1.586, 22.211]} = 59.628, P < 0.001$) for VarF_{TOT} with no significant interactions. As in earlier analyses, the steady-state intervals had the lower values of VarF_{TOT} as compared to the ramp intervals. Pairwise post hoc Tukey tests revealed that VarF_{TOT} values in intervals 1, 3, and 5 were significantly different from the values in intervals 2 and 4 at $P < 0.001$. Post hoc analysis did not reveal differences among intervals 1, 3, and 5 as well as intervals 2 and 4, $P > 0.05$. For the ΔV_{all-fingers} analysis, a main effect of *Interval* ($F_{[2.231, 31.227]} = 33.566, P < 0.001$) was found with no significant interactions: in the steady-state intervals, ΔV_{all-fingers} was not necessarily higher than in the ramp intervals. Pairwise post hoc Tukey tests did not reveal differences in ΔV_{all-fingers} between

interval 1 and intervals 3, 4, and 5 at $P < 0.001$. Pairwise post hoc Tukey tests also did not reveal differences between interval 2 and intervals 4 and 5, $P > 0.05$.

In order to examine the effects of symmetry, the following subset of conditions were used. The data from conditions $IM_R + IM_L$ and $RL_R + RL_L$ were averaged and used as “symmetric” conditions while the data from conditions $IM_R + RL_L$ and $IM_L + RL_R$ were averaged and used as “asymmetric” conditions. A two-way repeated-measures ANOVA with the factors *Interval* and *Symmetry* revealed only a main effect of *Interval* for both $VarF_{TOT}$ ($F_{[1.574, 33.064]} = 78.723$, $P < 0.001$) and $\Delta V_{all-fingers}$ ($F_{[2.361, 49.589]} = 53.343$, $P < 0.001$) without a significant interaction. For $VarF_{TOT}$ pairwise post hoc Tukey tests revealed that intervals 3 and 5 were significantly different from intervals 2 and 4 at $P < 0.001$. Post hoc analysis did not reveal differences between intervals 3 and 5 as well as intervals 2 and 4, $P > 0.05$. For $\Delta V_{all-fingers}$ pairwise post hoc Tukey tests revealed that the values in intervals 1 and 5 were significantly different from those in intervals 2 and 4 at $P < 0.001$. Post hoc analysis did not reveal differences between intervals 1 and 5 as well as intervals 2 and 4, $P > 0.05$.

Difference between one- and two-hand tasks

To compare the one-hand and two-hand tasks, we first examined the differences between the tasks that used the same of fingers, namely IMRL. The conditions $IMRL_R$, $IMRL_L$, $IM_R + RL_L$, and $IM_L + RL_R$ were used to examine the effects of finger distribution across the hands. The results were similar between the one-hand and two-hand tasks. A two-way repeated-measures ANOVA with the factors *Interval* and *Task* showed only a main effect of *Interval* for both $VarF_{TOT}$ ($F_{[2.007, 26.090]} = 37.454$, $P < 0.001$) and $\Delta V_{all-fingers}$ ($F_{[3.283, 42.680]} = 21.213$, $P < 0.001$) with no significant interaction. Pairwise post hoc Tukey tests revealed that $VarF_{TOT}$ values in intervals 1, 3, and 5 were significantly different from those in interval 4 at $P < 0.001$. Post hoc analysis did not reveal differences among intervals 1, 3, and 5 as well as intervals 2 and 5, $P > 0.05$. For $\Delta V_{all-fingers}$ pairwise post hoc Tukey tests revealed that the values in intervals 1, 3, and 5 were significantly different from those in intervals 2 and 4 at $P < 0.05$. Post hoc analysis did not reveal differences among intervals 1, 3, and 5 as well as intervals 2 and 4, $P > 0.05$.

Next, we analyzed performance of individual finger pairs involved in one- and two-hand tasks. In this analysis, the finger pair IM was examined across the conditions IM_R , IM_L , $IM_R + RL_L$, and $IM_L + RL_R$, while the finger pair RL was examined across the conditions RL_R , RL_L , $IM_R + RL_L$, and $IM_L + RL_R$. The $VarF_{TOT}$ and $\Delta V_{within-a-hand}$ values for each of the two finger pairs were averaged over the one-hand conditions and compared to the $VarF_{TOT}$ and $\Delta V_{within-a-hand}$ values for the same finger pair in the two-hand conditions.

Figure 7 illustrates the $\Delta V_{within-a-hand}$ profiles for three testing conditions of a representative subject. It shows much higher values of $\Delta V_{within-a-hand}$ for the one-hand task as compared to the two-hand task. The index showed modulation over the five segments in both tasks (a drop in $\Delta V_{within-a-hand}$ during the ramp segments); this modulation was much more pronounced in the one-hand task.

In order to analyze the data statistically, two-way repeated-measures ANOVAs were used with the factors *Interval* and *Task*. For $VarF_{TOT}$, a main effect of *Interval* ($F_{[2.475, 74.258]} = 74.607$, $P < 0.001$) and an interaction *Interval* $\times$ *Task* ($F_{[2.475, 74.258]} = 32.611$, $P < 0.001$) were found. The steady-state intervals showed the lowest $VarF_{TOT}$ values when compared to the ramp intervals for one-hand tasks. However, intervals 2, 3, and 4 showed the highest levels of $VarF_{TOT}$ for two-hand tasks, as seen in Fig. 8. Pairwise post hoc Tukey tests revealed that the values in intervals 1, 3, and 5 were significantly different from those in intervals 2 and 4 at $P < 0.005$. Post hoc analysis did not reveal differences between intervals 2 and 4, $P > 0.05$. For $\Delta V_{within-a-hand}$, main effects of *Interval* ($F_{[3.316, 99.490]} = 42.655$, $P < 0.001$), *Task* ($F_{[1, 30]} =$

55.726, $P < 0.001$), and the interaction *Interval* $\times$ *Task* ($F_{[3,316, 99,490]} = 10.045$) were found. Pairwise post hoc Tukey tests revealed that intervals the values in 1, 2, 4, and 5 were significantly different from those in interval 3 at $P < 0.001$. Post hoc analysis did not reveal differences among intervals 1, 2, 4, and 5, $P > 0.05$. In general, finger pairs in one-hand tasks exhibited significantly higher ΔV values as compared to the corresponding finger pair values for two-hand tasks, as seen in Fig. 9.

One-sample t tests with Bonferroni corrections were used to determine whether or not $\Delta V_{\text{within-a-hand}}$ values for the one-hand tasks were different from zero. Analysis showed that $\Delta V_{\text{within-a-hand}}$ in each of the time intervals was significantly different from zero ($t = 9.57, 4.00, 16.89, 3.83, 9.60$; $P < 0.01$). Similar one-sample t tests applied to the $\Delta V_{\text{within-a-hand}}$ values for the two-hand tasks showed that $\Delta V_{\text{within-a-hand}}$ was significantly different from zero only in interval 3 ($t = 5.25$; $P < 0.01$), and not different from zero in the other four time intervals.

Discussion

The major purpose of this experiment was to determine whether or not the CNS can organize force-stabilizing synergies simultaneously at two levels of a hypothetical motor control hierarchy involved in multi-finger two-hand actions, the upper level that distributes the task between the hands and the lower level that distributes each hand's action between the involved fingers (cf. the notion of the virtual finger, Arbib et al. 1985; MacKenzie and Iberall 1994). To address this issue, we compared within-a-hand force stabilizing synergies during one-hand and two-hand tasks. The main finding was that strong within-a-hand synergies were observed in one-hand tasks but not in two-hand tasks. We conclude, therefore, that the CNS organizes synergies stabilizing the overall task variable (total force in our experiments) only at the upper level of the hierarchy. Synergies at lower levels may be weaker or not present at all even if they are readily observed in similar tasks performed by one effector acting alone.

In the following discussion, we address the issue of hierarchies of synergies involved in natural movements. The contrasting results of our studies and earlier studies of static prehensile tasks (reviewed in Zatsiorsky and Latash 2004) allow us to offer a hypothesis on two types of synergies seen during natural actions, those that have to be created by the controller and those that are stored in memory and used as the foundation for the newly created synergies. We also discuss features of synergies related to steady-state and transient task fragments.

Hierarchies of synergies in natural movements

The notion of control hierarchies dates back at least half-a-century: a rather complex hierarchical scheme of motor control was suggested by Bernstein (1947, 1967, 1996). The second of the four (in some descriptions, five) levels of movement construction was termed "The Level of Muscular-Articular Links", or "Level of Synergies", or "Level B". Bernstein used the term "synergy" rather loosely, as a combined action of large groups of muscles. We use this term in a meaning, which is closer to the notion of "structural unit" as introduced by Gelfand and Tsetlin (1966). Further, this notion was developed into a principle of motor abundance (Gelfand and Latash 2002). According to this principle, the many apparently redundant elements typically involved in human actions (such as joints, muscles, motor units, etc.) are not eliminated or frozen (cf. Bernstein 1967; Vereijken et al. 1992) but are always all used to assure both stable and flexible performance of important variables. Synergies (structural units) represent neural organizations that produce a stable output variable by a coordinated action of many elements. Output variables analyzed in recent studies include the total force and total moment of force produced by a set of digits, endpoint coordinate, location of the center of pressure during standing, and many others (reviewed in Latash et al. 2003; Zatsiorsky and Latash 2004).

We would like to suggest a scheme that involves a hierarchical set of synergies (Fig. 10). Any synergy receives an input and produces an output. The input comes from a hierarchically higher synergy, while the output serves as an input into a hierarchically lower synergy. Figure 10 is certainly a major simplification. In particular, the hierarchy may branch to involve synergies that develop in parallel to those shown in the figure. For example, at any level, the output can be used as an input into a multi-muscle synergy, which will define activation levels of individual muscles. Those will project onto multi-motor-unit synergies, etc. For the purposes of this discussion, we assume that the input into the highest-level synergy comes from the “Task” and that the lowest-level synergy acts on the environment.

There are many studies that have demonstrated adjustments of the outputs of individual elements (effectors) to stabilize their combined action. Examples include the coordination of articulators during speech (Abbs and Gracco 1984), of arms during loading and unloading (Dufosse et al. 1985; Paulingnan et al. 1989), of joints during pointing, reaching, standing-up, and swaying (Domkin et al. 2002; Freitas et al. 2006; Scholz and Schöner 1999; Wang and Stelmach 1998), of muscles during standing and stepping (Krishnamoorthy et al. 2003; Wang et al. 2005), and of digits during pressing, grasping, and holding an object (Gao et al. 2005; Santello and Soechting 2000; Scholz and Latash 1998; Shim et al. 2005). Very few studies, however, have addressed synergies at different levels of an involved control hierarchy. Those include the studies of digit coordination during prehension (Baud-Bovy and Soechting 2001; Gao et al. 2005; Shim et al. 2005; Zatsiorsky et al. 2003) and of two-arm interaction during pointing (Domkin et al. 2002).

In particular, the coordinated action of fingers during prehensile tasks has been shown to stabilize the action of the virtual finger (VF), while the coordinated action of the VF and the thumb stabilized the gripping and rotational action components on the hand-held object (Shim et al. 2003a; Zatsiorsky et al. 2003). During two-arm pointing, the joints within each arm have been shown to stabilize the trajectory of the endpoint while across two-arms the vectorial distance between the endpoints was stabilized (Domkin et al. 2002, 2005).

Our results are unique in a sense that they show the lack of a synergy (or a very weak synergy) stabilizing the action of the low level effectors (finger pairs) in a two-hand task while such a synergy is clearly seen in a one-hand task. What could be the reasons? One major factor is the organization of visual feedback: the subjects received feedback on the total force but not on the force produced by a hand in a two-hand task. However, in all the cited studies of prehension, the subjects received no feedback on the action of the VF; nevertheless, its action was stabilized by combined action of the four fingers. During pointing tasks, the subject’s attention was drawn to relative motion of the two hands; nevertheless, multi-joint synergies stabilized each hand’s trajectory were seen (Domkin et al. 2002, 2005). Similarly, during postural tasks, multi-muscle analysis revealed the presence of synergies stabilizing shifts of the center of pressure (COP, the point of application of the resultant force acting on the body from the support surface) despite the fact that no feedback was available on the COP shifts (Krishnamoorthy et al. 2003; Wang et al. 2005). So, although the organization of the visual feedback could play a role in our experiments, it alone seems to be insufficient to explain the results.

We propose, therefore, the existence of two types of synergies. First, there are synergies that are used across many everyday actions. These include, for example, multi-muscle synergies involved in standing, multi-joint synergies involved in reaching and pointing, and multi-digit synergies involved in prehensile tasks. These synergies form a “library” that can be used to create novel synergies. Second, there are synergies that are novel and have to be created by the central nervous system based on a handful of practice trials. Apparently, the CNS is very good at this and can show strong synergies in rather artificial tasks (Latash et al. 2001; Shim et al. 2003b). However, it can use only synergies from the “library” as the foundation for a novel

synergy. Surprisingly, it seems to be unable to create two novel synergies at two hierarchical levels at the same time. As an earlier study suggests, massive practice may be required to lead to the creation of synergies at two hierarchical levels (Kang et al. 2004).

Do properties of elements matter?

We explored possible differences between the dominant and non-dominant hands, between finger pairs, and between tasks with symmetric and asymmetric finger involvement. Only the factor of finger pair showed major effects on the indices of multi-finger synergies. This is not a trivial result. In particular, recent studies of targeted reaching movements have suggested major differences between the dominant and non-dominant limbs in controlling movement trajectories and final endpoint locations (Sainburg and Schaefer 2004; Sainburg 2005). These studies have led to a hypothesis that the dominant arm is specialized for the control of movement dynamics (in particular, dealing with joint interaction torques) while the non-dominant arm is better suited for achieving the final, steady state, position. This hypothesis may be generalized to suggest that multi-element synergies are specialized for stabilization of steady-state values of performance for the non-dominant system, and for controlling their quick changes in the dominant system. Besides, Li et al. (2000) have shown differences in indices of finger interaction between the dominant and non-dominant hands. The lack of the effects of dominance may be due to the relative simplicity of our task (Sainburg and Schaefer 2004).

The lack of differences across symmetric and asymmetric two-hand tasks is also not trivial. Bimanual asymmetric tasks have been associated with both an increase in force deficit and an increased enslaving interaction between the two hands (Li et al. 2000, 2002). However, those results were obtained using maximal force production tests. It may well be that sub-maximal tasks are not associated with strong effects of symmetry of finger involvement.

The two finger pairs, IM and RL did show differences in their indices of force stabilization. In particular, the IM pair produced stronger synergies during steady-state force production when compared to the RL pair. Since force stabilization benefits from negative force co-variation between two fingers, this finding is in good agreement with evidence of higher independence of the index finger (Slobounov et al. 2002a, b) as well as higher enslaving of the ring and little fingers (Zatsiorsky et al. 1998).

Purposeful destabilization of performance?

A consistent finding over all conditions was the drop in ΔV indices of synergies during the ramp segments of the task as compared to the steady-state segments. This drop was typically associated with an increase in total force variance: an expected outcome of a drop in the strength of a synergy whose purpose is to decrease variability of the total force. Similar results were reported in earlier studies of multi-finger force production (Latash et al. 2002b; Shim et al. 2005). Destabilization of synergies has also been reported in a study of multi-muscle synergies stabilizing COP coordinate during quick COP shifts (Wang et al. 2006).

Two interpretations have been discussed for those findings. First, weakening of synergies have been described both in preparation to and in the process of a quick change in a performance variable that the synergy was expected to stabilize (Kim et al. 2006; Olafsdottir et al. 2005; Shim et al. 2005). These phenomena have been viewed as signs of a purposeful destabilization of the performance variable to facilitate its anticipated or ongoing change.

Second, a modeling work by Goodman and colleagues (2005) has shown that an increase in the rate of change of a performance variable may lead to a drop in its index of synergy even in the absence of changes at the control level. This study suggests that a drop in ΔV may be an artifact, a result of a high rate of force change. This may be partly true for our data. In particular,

even in two-hand tasks, the index of two-finger within-a-hand synergies ($\Delta V_{\text{within-a-hand}}$) that was close to zero showed a drop during the ramp portions of the task (see Fig. 7). The lack of a synergy in those conditions suggests that further purposeful destabilization of the total force was unlikely. On the other hand, the drop in ΔV in those conditions was much smaller than during one-hand two-finger tasks. So, it seems likely that both an increase in the rate of force change and a purposeful weakening of force-stabilizing synergies contributed to the observed dramatic drop in ΔV during the ramp segments.

Concluding comments

The demonstrated apparent inability of the central nervous system to organize synergies simultaneously at two levels of a control hierarchy is an unexpected result. As such, it asks for more scrutiny. In particular, it is possible that the visual feedback only on the total force output of the task fingers in the absence of feedback on the outputs of finger pairs in two-hand tasks led to this result. As discussed earlier, we see this explanation as unlikely. However, it has to be checked experimentally, for example in experiments with feedback on both individual hand and two-hand force. Generality of the main finding is another issue. Apparently, the main conclusion does not apply to one-hand grasping tasks with synergies demonstrated at both thumb-VF and individual finger level. Does it apply to tasks with a large object handled by two hands (eight fingers or four fingers of one hand and the thumb of the other hand)? Will two-finger synergies disappear if a subset of fingers from the other hand joins the task? We see these and other questions posed by the current results as the most important outcome of the study.

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Fig. 1.
An illustration of the sensor setup and visual feedback display for this experiment

Fig. 2.

An illustration of the task template, the five segments, and time intervals (*shorter dashed lines*) used for computation purposes

Fig. 3.

An illustration of force time profiles in two conditions by a representative subject. Data averaged over sets of 15 trials are shown. **a** Total force and forces produced by the finger pairs for the condition $IM_R + RL_L$. **b** Total force and individual finger forces for the condition IM_R . *I*, *M*, *R*, and *L* stand for the index, middle, ring, and little fingers, respectively. The subscripts *R* and *L* refer to the right and left hands

Fig. 4.

Total force variance across the five time intervals. The bars show data averaged across subjects within each condition and then averaged across all one- and two-hand tasks, respectively. Standard error bars are shown. An outline of the task template (in the background) is included for reference. Note the pronounced increase in the total force variance during the ramp segments

Fig. 5.

Time profiles $\Delta V_{\text{all-finger}}(t)$ computed over sets of 15 trials by a representative subject in two conditions. An outline of the template is shown for reference. **a** For the condition $\text{IM}_R + \text{RL}_L$. **b** For the condition IM_R . Abbreviations are the same as in Fig. 3. Note the highly positive values of the ΔV index during the steady-state segments and its drop during the ramp segments of the task

Fig. 6.

Indices $\Delta V_{\text{all-fingers}}$ were averaged across all one-hand tasks for the IM (*white bars*) and RL (*gray bars*) finger pairs separately. Standard error bars are shown. An outline of the task template (in the background) is included for reference. Abbreviations are the same as in Fig. 3. Note the similar modulation of ΔV for both finger pairs

Fig. 7.

Time profiles $\Delta V(t)$ computed over sets of 15 trials by a representative subject for pairs of fingers involved in one- and two-hand tasks **a** $\Delta V_{\text{within-a-hand}}$ for IM_R in the condition $\text{IM}_R + \text{RL}_L$. **b** $\Delta V_{\text{within-a-hand}}$ for IM_R in the condition IM_R . **c** $\Delta V_{\text{within-a-hand}}$ for RL_L in the condition $\text{IM}_R + \text{RL}_L$. **d** $\Delta V_{\text{within-a-hand}}$ for RL_L in the condition RL_L . Abbreviations are the same as in Fig. 3. Note the significantly higher ΔV values in the one-hand tasks; note also the more pronounced modulation of ΔV during the ramp segments of the task. Also, note that **a** and **c** show $\Delta V_{\text{within-a-hand}}$ for each hand involved in the bimanual condition $\text{IM}_R + \text{RL}_L$ while **b** and **d** show the same indices for the unimanual conditions IM_R and RL_L , respectively

Fig. 8.

Total force variance ($\text{Var } F_{\text{TOT}}$) computed over the five time intervals for each task and then averaged across subjects and across all one-hand two-finger conditions (*white columns*) and finger pairs within two-hand four-finger conditions (*gray columns*), respectively. Standard error bars are shown. An outline of the task template is shown for reference. Note the different modulation of $\text{Var } F_{\text{TOT}}$ for the finger pairs in one-hand tasks as compared to finger pairs in two-hand tasks

Fig. 9.

The index $\Delta V_{\text{all-fingers}}$, computed over the five time intervals for each task and then averaged across subjects and across all one-hand two-finger conditions (*white columns*) and finger pairs within two-hand four-finger conditions (*gray columns*), respectively. Standard error bars are shown. An outline of the task template is shown for reference. Note the stark difference in the index $\Delta V_{\text{all-fingers}}$ between the one-hand and two-hand tasks

Fig. 10.
A simplified illustration of the proposed hierarchy of synergies