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Emerging and disappearing synergies in a hierarchically controlled system

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Abstract

The purpose of the study was to explore the ability of the central nervous system (CNS) to organize synergies at two levels of a hypothetical control hierarchy involved in two-hand, multi-finger tasks. We investigated indices (ΔV) of finger force co-variation across trials as reflections of synergies stabilizing the total force (F_{TOT}). Subjects produced constant force with one or two finger-pairs (from one hand or two hands). In trials starting with one finger-pair, subjects added another finger-pair without changing F_{TOT} . In trials starting with two finger-pairs, subjects removed one of the finger-pairs without changing F_{TOT} . Adding or removing a finger-pair resulted in a transient drop in ΔV computed for the finger-pair that remained active throughout the trial. This drop in ΔV was seen simultaneously with force changes. Compared to the original steady-state, addition of a finger-pair led to a significant drop in ΔV at the newly established steady-state. This drop eliminated negative co-variation among finger forces that had stabilized F_{TOT} . In contrast, in trials starting with two finger-pairs, no negative co-variation between finger forces within-a-pair was seen. Removing a finger-pair led to the emergence of negative co-variation between finger forces at the new steady-state. The ΔV index computed across two finger-pairs confirmed the existence of negative force co-variation. The emergence and disappearance of force stabilizing synergies within a finger-pair may signal limitations in the ability of the CNS in forming synergies at two different hierarchical levels.

Keywords

Hand; Synergy; Finger; Force production; Bilateral action

Introduction

The notion of hierarchical control has been commonly invoked in studies of human movements (Bernstein 1947, 1967, 1996). In particular, the human hand has been commonly viewed as being controlled by (at least) a two-level hierarchy (Arbib et al. 1985). At the upper level of the hierarchy, the total force and the total moment of force produced on the hand-held object are distributed between the actions of the thumb and the virtual finger (VF, an imagined finger with the mechanical action equal to that of all the fingers of the hand, Arbib et al. 1985; Mackenzie and Iberall 1994). At the lower level, the action of the VF is distributed among the four fingers of the hand.

Several studies investigated force- and moment-of-force-stabilizing synergies at the two hierarchical levels (Baud-Bovy and Soechting 2001; Gao et al. 2005; Santello and Soechting

2000; Shim et al. 2005a, b; Zatsiorsky et al. 2003; reviewed in Zatsiorsky and Latash 2004). In those studies, synergies were defined as neural organizations leading to co-variation in variables produced by elements of a system (elemental variables) that stabilized potentially important performance variables (Gelfand and Latash 1998; Latash et al. 2002b). In particular, the forces and moments produced by the thumb and VF have been shown to co-vary to stabilize the total force and the total moment of force exerted on the hand-held object (Shim et al. 2005a; Zatsiorsky et al. 2003). At the lower level of the hierarchy, forces produced by individual digits have been shown to co-vary to stabilize the VF force magnitude, point of force application, and direction (Gao et al. 2005; Latash et al. 2002a).

Two recent studies have documented a surprising lack of ability of the central nervous system (CNS) to organize force stabilizing synergies at two levels of a control hierarchy simultaneously in two-hand four-finger tasks (Gorniak et al. 2007; Kang et al. 2004). In particular, in one-hand two- and four-finger tasks this requires the production of an accurate pattern of the total force, commands to individual fingers have been shown to co-vary across repetitive trials such that the total force profile showed relatively low variability (a force-stabilizing synergy, see Latash et al. 2001, 2002a; Scholz et al. 2002). However, when a similar task was performed by two finger-pairs, one pair per hand, fingers within each hand failed to show co-variation stabilizing the contribution of that hand to the total force. These observations have resulted in a hypothesis that the CNS is able to create new synergies at only one level of a control hierarchy at a time.

The purpose of the current study has been to explore this controversial hypothesis in two ways. The previous study (Gorniak et al. 2007) used only accurate force production tasks where the finger set explicitly involved in force production remained unchanged over the duration of a trial. Hence, it remained unknown whether force stabilizing synergies within a finger-pair can emerge and disappear when another finger-pair is removed from or added to the task. It was also unclear whether the counter-intuitive lack of within-a-finger pair synergies is specific to two-hand action or it can be observed when the four fingers of a hand are united into finger-pairs by instruction. Clarifying these issues is important to explore the generality of the original findings and their possible relation to hierarchical control.

Correspondingly, we tested two main hypotheses. First, we hypothesized that turning a one-hand accurate force production task into a two-hand task would lead to disappearance of a within-a-hand force stabilizing synergy. Along similar lines, we also hypothesized that when one hand is removed from a two-hand task, a previously absent within-a-hand synergy would emerge; this assumption is directly based on the results of Gorniak et al. (2007).

Second, we hypothesized that the phenomena of emerging and disappearing synergies would not be limited to two-hand tasks but could also be observed in one-hand tasks if the four fingers are separated into two pairs by instruction. If the two hypotheses formulated in the previous paragraph are supported in one-hand two-pair tasks, this would provide additional support for the idea that hierarchical control is to blame for the lack of within-a-finger-pair synergies, not the simultaneous involvement of two extremities in a task.

Methods

Participants

Five male and five female students served as subjects in this study. Average data for the subjects were (mean $\pm$ SD): 27 $\pm$ 3 years of age, 1.71 $\pm$ 0.11 m in height, 70.9 $\pm$ 12.8 kg in mass, 18.8 $\pm$ 1.8 cm for right hand length, 8.5 $\pm$ 1.0 cm for right hand width, 18.9 $\pm$ 1.9 cm for left hand length, and 8.3 $\pm$ 1.0 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 metacarpophalangeal (MCP) joints. All subjects were strongly 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 tips of 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 (14 cm × 9 cm each) in a groove on a wooden board. The two frames were spaced 40 cm apart. The sensors were medio-laterally spaced 3 cm apart from each other within the aluminum frames. The position of the sensors in the anterior–posterior direction could be adjusted within 6 cm in order to fit individual subject hand anatomy, see Fig. 1. At the beginning of each trial, the signal from each of the sensors was set to zero. Subjects were instructed to rest their fingers on the sensors, but to apply no active force prior to each trial.

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 were secured to the wooden 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-fitted 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 200 Hz with a National Instruments A/D board (NIPCI-6023E, National Instruments, Austin, TX, USA) and LabView-based program (LabView 6.1, National Instruments, Austin, TX, USA).

Procedure

The experiment consisted of two control trials and a main set of tasks. In the control trials, the subjects were required to produce maximal voluntary contraction (MVC) force. In these trials, the subjects were required to press with all eight fingers “as hard as possible”. Each MVC trial started with the subject sitting quietly with the hands resting on the sensors. A sound signal was given and then a cursor showing the total force produced by all eight fingers started to move over the screen. The subject was given a time interval of 3 s to reach maximal force by pressing down with the fingers. There were intervals of at least 30 s between successive MVC trials. Two MVC trials were collected and the trial with the highest total peak force was selected for setting the subsequent tasks. The peak force value obtained in the MVC trials (MVC_8) was used to set up the template for the main tasks.

There were two main sets of tasks that each included three conditions. The two main sets of tasks were performed under two instructions, ADD or REMOVE. For the ADD instruction, subjects were instructed to produce and maintain 5% of MVC_8 with a designated finger-pair

on the right hand for 5 s, then quickly and smoothly add another designated finger-pair such that the total force was to remain unchanged and to keep the force at the 5% of MVC₈ level for another 5 s. For the REMOVE instruction, subjects were instructed to produce and maintain 5% of MVC₈ with two designated finger-pairs for 5 s, then quickly relax one of the finger-pairs and maintain the 5% of MVC₈ level with only one finger-pair for the remaining 5 s of the trial. There was a visual cue on the screen at the 5 s mark (i.e., halfway through the trial) visible throughout each trial, indicating that the subject would need to either add or remove a finger-pair at that point in the trial. We tested the following conditions in the ADD set: ADD IM_L to IM_R, ADD RL_L to RL_R, and ADD RL_R to IM_R (I–index, M–middle, R–ring, and L–little fingers; subscripts R and L refer to the right and left hand respectively). Similarly, we tested the following conditions in the REMOVE set: REMOVE IM_L from IM_R + IM_L, REMOVE RL_L from RL_R + RL_L, and REMOVE RL_R from IM_R + RL_R. The 5% MVC₈ level was chosen for this particular experiment in order to keep the subjects from experiencing muscular fatigue. Finger-pairs for the experimental trials were selected assuming no differences between the dominant and non-dominant hands in terms of a force-production task, as demonstrated in Gorniak et al. (2007).

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 level (see Fig. 1), and the task was to follow the shown profile with the cursor.

In each condition, subjects performed 15 trials with 8-s intervals between the trials. There were 3-min intervals after each 15-trial series. Overall, there were 90 total 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 three practice trials per task plus or minus one practice trial. The conditions were presented in a block randomized order across subjects. Each condition was presented as a block of trials; blocks were randomized across the subjects. Only trials in which the subject failed to add a finger-pair or remove a finger-pair (depending on the task instruction) were rejected. On average, less than one trial was rejected per condition for each subject.

Data analysis

The data were processed off-line 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 2nd order, zero-lag Butterworth filter.

The 15 trials within each series were aligned based on the onset of force increase by IM_L, RL_L, or RL_R (for each of the corresponding conditions, respectively) for the ADD instruction and the onset of force decrease by IM_L, RL_L, or RL_R for the REMOVE instruction. For the ADD instruction, the onset of force increase was defined as the time at which the first time derivative of the force of the designated finger-pair reached 10% of its peak value in that trial. For the REMOVE instruction, the onset of force decrease was defined as the time at which the first derivative of the force (with respect to time) of the designated finger-pair “removed from the task” reached 10% of the peak absolute value of the force time derivative.

Further, the following time-varying variables were computed at each point in time for each subject over the 15 trials within each condition.

- (1) The total force, $F_{TOT}(t)$ of explicitly involved task fingers, and its variance, $VarF_{TOT}(t)$;
- (2) the sum of variances of each individual finger force, $\Sigma VarF_i(t)$;

- (3) variance of each hand's force, $\text{Var}F_{\text{Hand}}(t)$. Hand's force was computed as the sum of the forces produced by the explicitly involved fingers of that hand; and
- (4) the sum of variances of individual finger forces within a hand produced by the explicitly involved fingers of that hand, $\Sigma \text{Var}F_{i\text{-hand}}(t)$.

For quantitative assessment of multi-finger synergies, we used an index of co-variation computed as the normalized difference between the variance of the total output of a set of effectors (fingers or hands) and the sum of the variances of the forces produced by the individual effectors. According to the Bienaymé theorem (Loève 1955), these two values should be equal to each other, unless there is co-variation among the outputs of the effectors. In particular, an index of force-stabilization by all the explicitly involved fingers was computed as:

$\Delta V_{\text{task-fingers}}(t) = [\Sigma \text{Var}F_i(t) - \text{Var}F_{\text{TOT}}(t)] / \Sigma \text{Var}F_i(t)$. Under the ADD instruction, $\Delta V_{\text{task-fingers}}$ initially only accounted for the finger-pair that started the action (either IM_R or RL_R). After the onset of force addition by the added pair (IM_L , RL_L , or RL_R), $\Delta V_{\text{task-fingers}}$ accounted for all four fingers in the task. Likewise under the REMOVE instruction, $\Delta V_{\text{task-fingers}}$ initially accounted for all four fingers in the task ($\text{IM}_R + \text{IM}_L$, $\text{RL}_R + \text{RL}_L$, or $\text{IM}_R + \text{RL}_R$), but after the onset of force decrease by the removed pair, $\Delta V_{\text{task-fingers}}$ accounted for only the finger-pair (either IM_R or RL_R) that continued to maintain the force output.

An index of force stabilization between the two hands was computed as: $\Delta V_{\text{two-hand}}(t) = [\Sigma \text{Var}F_{\text{Hand}}(t) - \text{Var}F_{\text{TOT}}(t)] / \Sigma \text{Var}F_{\text{Hand}}(t)$ (only for two-hand tasks). An index of force stabilization between two fingers of a finger-pair was computed as: $\Delta V_{\text{within-a-pair}}(t) = [\Sigma \text{Var}F_{i\text{-hand}}(t) - \text{Var}F_{\text{Hand}}(t)] / \Sigma \text{Var}F_{i\text{-hand}}(t)$. For two-hand tasks, this index was computed for each hand separately. For tasks that involved two finger-pairs within a hand (IM and RL), the index was computed for each of the two finger-pairs.

Note that all ΔV indices were normalized by the sum of variances of the forces produced by corresponding sets of effectors (fingers for $\Delta V_{\text{task-fingers}}$ and $\Delta V_{\text{within-a-pair}}$ and hands for $\Delta V_{\text{two-hand}}$) to allow for comparisons among different ΔV indices across conditions and subjects. 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. 2005b). Large positive ΔV values correspond to larger amounts of negative co-variation—a stronger synergy. If $\Delta V \leq 0$, this 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.

The onset of $\Delta V_{\text{within-a-pair}}$ changes was defined for both the ADD and REMOVE instructions as the time at which the first time derivative of the $\Delta V_{\text{within-a-pair}}$ of the designated finger-pairs reached 10% of its peak absolute value within ± 400 ms of the onset of force change, as defined above. This time window was selected to analyze the relative timing of the force and ΔV changes (see Sect. "Results").

Three stages were considered for each condition for both the ADD and REMOVE instructions. The steady-state stage prior to the addition or removal of a finger-pair will be referred to as Stage-1, while the steady-state stage following the addition or removal of a finger-pair will be referred to as Stage-2. During Stage-1, the interval 0.5–1.0 s prior to the onset of force change was used to calculate the averages of force and force synergy indices. Similarly, during Stage-2, the interval 2.0–2.5 s following to the onset of force change was used to calculate the averages of force and force synergy indices. This interval was selected in order to ensure that subjects had enough time to stabilize their force output. The third (transient) stage corresponded to the time of finger force removal and addition when major quick changes in force variance and synergy indices were seen (cf. Li et al. 2002; see Sect. "Results").

The averages of F_{TOT} , and ΔV indices were computed during both Stage-1 and Stage-2 for each task and each subject. The average of $\Delta V_{two-hand}$ was computed only in stages in which two hands were involved (Stage-2 for the ADD instruction and Stage-1 for the REMOVE instruction). The average of $\Delta V_{within-a-pair}$ (for IM_L , RL_L , and RL_R , with respect to the given tasks listed in Sect. "Procedure") was found only in the stages in which these finger-pairs were involved (in Stage-2 for the ADD instruction and in Stage-1 for the REMOVE instruction).

Statistics

The data are presented in the text and figures as means and standard errors. Repeated-measures analyses of variance (ANOVAs) were performed with the factors: *Stage* (two or three levels, Stage-1, Stage-2, and transient stage), *Action* (two levels, ADD and REMOVE), *Hands* (two levels, one and two; to denote how many hands are involved in the task), and *Finger-Pair* (two levels, IM and RL). One-sample *t*-tests (with Bonferroni corrections) were used to compare $\Delta V_{within-a-pair}$ to 0 in order to check for a presence of within-a-pair force-stabilizing synergies. Paired *t*-tests (with Bonferroni corrections) were used to compare the onset of force change with the onset of $\Delta V_{within-a-pair}$ for each testing condition. 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 analysis of pair-wise comparisons was performed using Bonferroni statistics to analyze the significant effects of ANOVAs.

Results

General force and variance time profiles

All subjects were able to perform the task without overt difficulty. Overall, subjects were excellent at the tasks, with the average force level across all subjects and tasks being 5.057% of MVC_8 (the target value was 5%) while RMS was 0.001%, computed for seconds 2–10 of the trials (all subjects had reached a steady-state force level within 2 s of trial initiation). An example of typical performance by a representative subject is shown in Fig. 2. Total force (F_{TOT}) time profiles, averaged over 15 trials, as well as variance of total force ($VarF_{TOT}$) and sum of finger force variance ($\Sigma VarF_i$) profiles are shown for the task ADD IM_L to IM_R (panel a) and for the task REMOVE IM_L from $IM_R + IM_L$ (panel b).

There were brief transient deviations of the total force from the required level when a finger-pair was added or removed. These deviations were not consistent across subjects and tasks. The onsets of force change by the finger-pairs "added to" and "removed from" the task were not significantly different from the occurrence of the visual cue in the trials (at the 5-s mark); the average onset of force change was 4.965 ± 0.066 s. $VarF_{TOT}$ and $\Sigma VarF_i$ both increased during the initiation of force production as well as in the transient stage of the tasks (under both the ADD and REMOVE instructions). Note that $VarF_{TOT}$ was much lower than $\Sigma VarF_i$ during both steady-state stages (Stage-1 and Stage-2, see Sect. "Methods") in which either one hand or two hands maintained the 5% MVC force level. This finding was consistent for both ADD and REMOVE instructions.

Overall, $VarF_{TOT}$ was smaller in Stage-1 as compared to Stage-2. This was confirmed by a two-way repeated measures ANOVA with factors: *Stage* and *Action*. Only the main effect of *Stage* [$F_{(1, 58)} = 22.638$, $P < 0.001$] was found without a significant interaction.

The sum of individual finger force variances, $\Sigma VarF_i$ was approximately the same in Stage-1 and Stage-2 for the ADD conditions, however it was smaller in Stage-1 as compared to Stage-2 the REMOVE conditions. This was confirmed by a two-way repeated measures ANOVA with factors: *Stage* and *Action*. Main effects of *Stage* [$F_{(1, 58)} = 20.183$, $P < 0.001$], *Action* [$F_{(1, 58)} = 8.000$, $P < 0.01$], and the interaction *Stage* $\times$ *Action* [$F_{(1, 58)} = 35.970$, $P < 0.001$] were found.

Pair-wise post hoc Tukey tests revealed that the interaction was due to the fact that during Stage-1 the REMOVE instruction yielded higher $\Sigma Var F_i$ compared to the ADD instruction, while in Stage-2 the opposite was true ($P < 0.001$) as shown panel a in Fig. 3.

Within-a-pair synergies during bimanual force production

Overall, indices of within-a-pair synergies were low and typically close to 0 or even negative while two hands worked together in a force production task. This finding was confirmed by a three-way repeated measures ANOVA on the index $\Delta V_{\text{within-a-pair}}$ with the factors: *Stage*, *Action*, and *Finger-Pair*. Main effects of *Stage* [$F_{(1,56)} = 33.507$, $P < 0.001$] and the interaction *Stage* $\times$ *Action* [$F_{(1,56)} = 205.312$, $P < 0.001$] were found. Pair-wise post hoc Tukey tests revealed that under the ADD instruction, $\Delta V_{\text{within-a-pair}}$ was significantly higher in Stage-1 compared to Stage-2 and vice versa for the REMOVE conditions; both at $P < 0.001$. This finding is illustrated in panel b of Fig. 3.

In order to confirm that the low $\Delta V_{\text{within-a-pair}}$ values during two-hand phases of the tasks were indicative of a lack of force stabilizing synergies, we performed a series of one-sample *t*-tests with Bonferroni corrections comparing $\Delta V_{\text{within-a-pair}}$ to 0. The tasks ADD IM_L to IM_R and ADD RL_L to RL_R showed distinctly different $\Delta V_{\text{within-a-pair}}$ values from 0 ($t = -9.63$ and $t = -3.01$, $P < 0.001$ and $P < 0.01$, respectively); however the 95% confidence intervals showed that the $\Delta V_{\text{within-a-pair}}$ values for the finger-pairs in these two tasks were actually negative. In the remaining conditions, $\Delta V_{\text{within-a-pair}}$ indices were not significantly different from 0. The overall mean and standard error of $\Delta V_{\text{within-a-pair}}$ for those conditions was -0.0608 ± 0.0717 (no units, due to normalization).

Comparison of one-hand vs. two-hands tasks

Next, we examined whether or not indices of within-a-pair force-stabilizing synergies differed depending on the number of hands (one vs. two) involved in the task. In order to do so, we only examined the conditions that involved the IMRL set of fingers, across two hands or within a hand, IM_R + RL_L and IM_R + RL_R. Both conditions were characterized by qualitatively similar results. When a pair of fingers worked alone (Stage-1 for the ADD condition and Stage-2 for the REMOVE condition), the forces produced by the two fingers showed strongly positive $\Delta V_{\text{within-a-pair}}$. When the same pair worked with another pair, no matter if they were from the same hand or from the other hand (Stage-2 for the ADD condition and Stage-1 for the REMOVE condition), $\Delta V_{\text{within-a-pair}}$ dropped to 0 or even to negative values.

However, there were quantitative differences depending on whether the four fingers belonged to one hand or to two hands. In particular, in Stage-1, the one-hand task showed higher absolute values of $\Delta V_{\text{within-a-pair}}$ for both ADD and REMOVE instructions as compared to two-hand tasks. In contrast, during Stage-2, tasks involving two hands showed higher absolute values of $\Delta V_{\text{within-a-pair}}$ for both ADD and REMOVE instructions as compared to tasks involving only one hand. Both of these findings are illustrated for Stage-1 and Stage-2 separately in panels c and d of Fig. 3.

These findings were confirmed with a three-way repeated measures ANOVA with the factors: *Stage*, *Action*, and *Hands*. Main effects of *Stage* [$F_{(1,36)} = 35.318$, $P < 0.001$], the interaction *Stage* $\times$ *Action* [$F_{(1,36)} = 175.579$, $P < 0.001$], and the interaction *Action* $\times$ *Hands* [$F_{(1,36)} = 6.387$, $P < 0.05$] were found. The result for the *Stage* $\times$ *Action* interaction is similar to that described earlier and illustrated in panel b of Fig. 3 while the *Action* $\times$ *Hands* interaction is illustrated for Stage-1 and Stage-2 separately in panels c and d of Fig. 3.

A transient drop in $\Delta V_{\text{within-a-pair}}$ was seen in the finger-pair that was active in both stages of the tasks across both the ADD and REMOVE instructions (illustrated via an increase in both

$\text{Var}F_{\text{TOT}}$ and $\Sigma\text{Var}F_i$ in Fig. 2). Overall, this transient in $\Delta V_{\text{within-a-pair}}$ reached significantly lower values than the values of $\Delta V_{\text{within-a-pair}}$ in either of the two stages of the task. However, the magnitude of the drop depended on whether fingers within one hand or between two hands were involved in the given tasks. Namely, the transient drop in ΔV was more pronounced in two-hand tasks. This finding was confirmed using a three-way repeated measures ANOVA with the factors *Stage* (three levels; Stage-1, transient, and Stage-2), *Action*, and *Hands*. Main effects of *Stage* [$F_{(2,112)} = 113.467, P < 0.001$], *Hands* [$F_{(1,56)} = 5.15, P < 0.05$], and the interactions *Stage* $\times$ *Action* [$F_{(2,112)} = 119.888, P < 0.001$], *Stage* $\times$ *Hands* [$F_{(2,112)} = 4.531, P < 0.05$], and *Action* $\times$ *Hands* [$F_{(1,56)} = 6.749, P < 0.05$] were found. Pair-wise post hoc Tukey tests revealed that ΔV indices in all three stages (Stage-1, transient, and Stage-2) were significantly different from each other at $P < 0.001$. Pair-wise post hoc Tukey tests also revealed that using one hand in a task resulted in higher values of $\Delta V_{\text{within-a-pair}}$ across all time stages at $P < 0.05$.

The *Stage* $\times$ *Action* interaction indicated that under the ADD instruction, $\Delta V_{\text{within-a-pair}}$ was a positive number close to unity in Stage-1 (0.767 ± 0.058), then it underwent a drop during the transient stage, and remained a value less than 0 during Stage-2 (-0.287 ± 0.059). Under the REMOVE instruction, $\Delta V_{\text{within-a-pair}}$ was close to 0 in Stage-1 (-0.052 ± 0.058), then it underwent a further drop during the transient stage, and finally became a positive value during Stage-2 (0.389 ± 0.059). These changes in $\Delta V_{\text{within-a-pair}}$ can be seen in panel a of Fig. 4. The *Stage* $\times$ *Hands* interaction indicates that $\Delta V_{\text{within-a-pair}}$ for one hand performing a task was generally higher across all stages when compared to two hands performing a task, as shown in panel b of Fig. 4. The *Action* $\times$ *Hands* interaction showed that one hand performing under the ADD instruction had higher absolute values of $\Delta V_{\text{within-a-pair}}$ compared to the REMOVE instruction as shown in panel c of Fig. 4.

The index $\Delta V_{\text{two-hand}}$ existed only during stages of the task where two hands participated in the force production. In order to determine whether or not the two hands were united in a force stabilizing synergy, one-sample *t*-tests with Bonferroni corrections were performed in order to compare $\Delta V_{\text{two-hand}}$ to 0. Each of the four bimanual conditions examined (ADD IM_L to IM_R, ADD RL_L to RL_R, REMOVE IM_L from IM_R + IM_L, and REMOVE RL_L from RL_R + RL_L) showed distinctly positive values ($t = 18.19, t = 28.02, t = 13.59, t = 17.27$; with $P < 0.001$ for each condition, respectively). The overall mean and standard error of $\Delta V_{\text{two-hand}}$ for these conditions was 0.8665 ± 0.0293 .

The index $\Delta V_{\text{task-fingers}}$ was examined in order to determine whether or not the fingers explicitly involved in the task were united in a force-stabilizing synergy across the three stages of the tasks under both the ADD and REMOVE instructions. In order to determine this, a two-way repeated measures ANOVA was performed with the factors: *Stage* (three levels) and *Action*. Main effects of *Stage* [$F_{(1,632,94,681)} = 231.848, P < 0.001$], *Action* [$F_{(1,58)} = 54.851, P < 0.001$], and the interaction *Stage* $\times$ *Action* [$F_{(1,632,94,681)} = 34.130, P < 0.001$] were found. Pair-wise post hoc Tukey test revealed that the indexes during all three stages were significantly different from each other at $P < 0.001$. It was found that $\Delta V_{\text{task-fingers}}$ was largest during Stage-1, smaller during Stage-2, and smallest during the transient stage. Pair-wise post hoc Tukey test revealed that the ADD instruction yielded higher $\Delta V_{\text{task-fingers}}$ indices as compared to the REMOVE instruction. The *Stage* $\times$ *Action* interaction showed that while the ADD instruction showed lower values of $\Delta V_{\text{task-fingers}}$ during Stage-1 as compared to the REMOVE instruction, the $\Delta V_{\text{task-fingers}}$ indices during the transient stage and Stage-2 were larger than $\Delta V_{\text{task-fingers}}$ for the REMOVE instruction, as seen in panel d of Fig. 4.

Relative timing of ΔV changes

To explore the relative timing between the changes in force and in the index of force stabilizing synergy (ΔV), the difference between the onset of changes in the force produced by the

designated finger-pair (either an increase or decrease, depending on the task instructions) and the onset of $\Delta V_{\text{within-a-pair}}$ changes were compared. To remind, both onset values were defined as the time when the first derivative for that particular variable reached 10% of its peak value (see Sect. “Methods”). There was substantial variability across subjects in the relative timing of ΔV changes with respect to force changes. Across all subjects, on average, $\Delta V_{\text{within-a-pair}}$ lagged the onset of force change by a time interval under 100 ms (95.5 ± 59.1 ms for the right hand in the ADD instruction, 31.8 ± 70.7 ms for the right hand in the REMOVE instruction, and 32.3 ± 46.6 ms for the left hand in the REMOVE instruction). Paired *t*-tests (with Bonferroni corrections) revealed that none of these values were significantly different from zero at the $\alpha = 0.05$ level.

Discussion

In Sect. “Introduction”, we formulated a set of specific hypotheses based on a general hypothesis that the CNS is able to organize force-stabilizing synergies at only the upper level of a control hierarchy (Gorniak et al. 2007). To test the hypotheses, we designed a task that was expected to involve a two-level hierarchy; that is a two-hand, four-finger accurate force production task. Since the structure of the control scheme is not directly observable, we assumed that such tasks were associated with a two-level control hierarchy. At the higher level of this hierarchy, the task is distributed between the two hands; while at the lower level, action of each hand is distributed between the fingers within that hand. Results of our experiments can be viewed as providing indirect support for the assumed two-level control scheme.

All the specific hypotheses formulated in Sect. “Introduction” have been confirmed in the experiments. In particular, adding a finger-pair from one hand to a constant force production task performed by a finger-pair from the other hand led to the disappearance of a within-a-hand, two-finger synergy stabilizing the total force produced by that hand. Along similar lines, removing a finger-pair from one hand from a two-hand, four-finger force production task led to the emergence of a within-a-hand two-finger force stabilizing synergy. The phenomena of emerging and disappearing synergies was not due to the bilateral, two-hand nature of the tasks as shown in experiments where finger-pairs were added or removed keeping the force production task to fingers of one hand only.

While practice can indeed lead to learning effects and changes in multi-finger force stabilizing synergies, we do not believe that our results were in any major way affected by effects of learning since such effects are expected to occur after numerous repetitions (Kang et al. 2004; Latash et al. 2003). In our experiments, repetitions were relatively few, and the random-blocked design also helped to avoid learning effects.

In the following discussion, we address a number of issues related to the origin of such apparent emergence and disappearance of synergies.

Hierarchical control of multi-element systems

Virtually all natural human motor actions involve redundant sets of elements (Turvey 1990; Latash 1996). The concept of hierarchical control in motor control (Bernstein 1947; developed later by Gelfand and Tsetlin 1966) has been viewed as a means of decreasing the number of variables manipulated by the controller at each control level of a hierarchy thus alleviating the problem of motor redundancy. However, the redundancy could not be completely eliminated by introducing control hierarchies, and the idea of elimination of redundant degrees-of-freedom has dominated over the past 50 years (Bernstein 1947, 1967; Turvey 1990; Vereijken et al. 1992). In particular, optimization approaches have been used to define unique solutions in a variety of tasks (for a recent review see Prilutsky and Zatsiorsky 2002) including prehensile tasks (Zatsiorsky et al. 2002). These approaches, however, by their search for unique optimal

solutions, do not address issues of across trials variability, which are central to the notion of synergies.

An alternative approach has been formulated recently as a principle of abundance (Gelfand and Latash 1998), which states that the redundant elements participating in virtually all natural motor actions are not eliminated but always used in order to ensure both stability and flexibility necessary for successful actions in poorly predictable environments. According to this approach, at each level of a hierarchy, synergies are formed to produce a one-to-many mapping of an input signal (task) to signals to individual elements (effectors). Such synergies can be revealed in co-variations among elemental variables that stabilize or do not stabilize the overall output of a set of elements (reviewed in Latash et al. 2007).

The principle of abundance is readily compatible with the idea of hierarchical control. At each level of the hierarchy, a one-to-many mapping ensures a flexible combination of output (elemental) variables that produces a required stable value of the total output of the system defined by its input. Such flexibility has many advantages including a possibility to perform several tasks simultaneously (cf. principle of superposition reviewed in Zatsiorsky and Latash 2004).

Previously, we have proposed that there could be two types of synergies: those that are used in everyday actions (highly practiced) and those that are novel and have to be assembled by the CNS based on little practice (Gorniak et al. 2007). While the CNS can indeed create novel synergies (Latash et al. 2001; Shim et al. 2003), it appears to be unable to generate novel synergies at two hierarchical levels simultaneously unless given extensive amounts of practice (Kang et al. 2004). In the current study, we purposefully used a very simple task, constant force production by a set of fingers, but varied the involvement of hands and finger-pairs to manipulate the hypothetical control scheme. In all conditions, as soon as a two-finger task turned into a two-pair task, involving one or two hands, the force-stabilizing synergies disappeared (Fig. 3). We interpret these observations as resulting from a change in the control structure, namely an addition of a new hierarchically higher level that distributes the task between the finger-pairs in addition to distributing each finger pair's action between the fingers. An opposite effect was also observed: The emergence of a synergy when a two-pair task turned into a one-pair task (Fig. 3).

Good and bad variability in hierarchical control

Changes in force-stabilizing synergies with a change in the number of finger-pairs involved in an accurate force production task may be interpreted using the notions of good and bad variability. Consider the task of constant total force production by two elements (for example, fingers). In the space of forces produced by each of the elements, a line with a negative slope (solid line in Fig. 5a) corresponds to perfect task execution. Hence, any variability of finger forces that is limited to that line may be viewed as “good” since it leads to no errors in the total force. Variability that leads to deviations from the line (parallel to the dashed line with a positive slope in Fig. 5a) is going to violate the total force and in that sense may be addressed as “bad”. Since the two lines are orthogonal, any distribution of data points across trials may be described with two variability indices corresponding to the variance along each of the two lines. The earlier introduced definition of a force-stabilizing synergy corresponds to a situation when “good variance” is larger than “bad variance” ($V_{\text{GOOD}} > V_{\text{BAD}}$), i.e., the two forces co-vary negatively (see Latash et al. 2007).

The illustration in Fig. 5 suggests that a force-stabilizing synergy depends on the relative magnitudes of two indices, variability of the total force (V_{BAD}) and variability that does not affect total force (V_{GOOD}). Imagine now that a two-hand synergy is organized to stabilize the total force (as in the current study with two-hand force production). The presence of such a

synergy means that V_{GOOD} is substantially larger than V_{BAD} . Note that the magnitude of V_{GOOD} is higher when the range of changes in the forces produced by individual hands is larger (panel b in Fig. 5). However, an increase in the range of force produced by a hand by definition leads to an increase in its “bad variability” (panel c in Fig. 5). Hence, the most straightforward method of creating a two-hand force-stabilizing synergy, that is an increase in its V_{GOOD} is expected to be reflected in an increase in V_{BAD} for each of the participating finger-pairs. This may be expected to result in a drop of the index of force-stabilizing synergies for each finger-pair (each hand) as observed in our experiments.

This simple analysis suggests that there is an inherent trade-off between synergies that stabilize the output of each of the control levels in a hierarchy. This trade-off can be overcome if the controller manages to keep V_{GOOD} relatively low at the higher level of the hierarchy while still preserving the inequality $V_{\text{GOOD}} > V_{\text{BAD}}$. This may require extensive practice as shown by one of the previous studies, in which force-stabilizing synergies emerged after 3 days of practice (Kang et al. 2004). However, it is possible that our method of feedback to the subjects may have influenced the trade-off between synergies at the two hierarchical levels. In the current experiment, subjects were presented with total force feedback, not finger-pair feedback. It is feasible that finger-pair feedback may result in synergies at the finger-pair level. This hypothesis should be explored in future experiments.

Possible mechanisms involved in synergies

Both biomechanical and neurophysiological factors can potentially contribute to multi-finger synergies. With respect to biomechanics, it is known that the digits within the hand are coupled via multiple anatomical structures. The digits are connected by soft tissues within the palm and between the digits (von Schroeder and Botte 1993), as well as by the multi-tendon, multi-digit extrinsic hand muscles. The tendons from these muscles are known to transmit forces among each other (Schieber et al. 2001). Motor unit synchrony between the compartments of such muscles has also been shown to contribute to simultaneous activation of digits within a hand (Kilbreath and Gandevia 1994; Reilly and Schieber 2003; Santello and Fuglevand 2004; Winges et al. 2006). These mechanisms are expected to lead to positive co-variation of forces produced by individual digits of a hand. As such, they are unlikely to lead to force-stabilizing synergies that require negative co-variation of finger forces. Indeed, these mechanisms have to be overpowered by synergy producing mechanisms.

The primary motor cortex (M1) is one of the most conspicuous structures potentially contributing to the formation of multi-digit synergies. Studies by the group of Schieber (Schieber 1990, 2002; Schieber and Hibbard 1993; Schieber and Santello 2004) suggest that synergies may be controlled by spatially scattered but physiologically similar subsets of neurons within M1. The projections of the corticospinal tract suggest that there may be a large variety of muscle combinations that could be controlled by subsets of neurons in M1 (Schieber and Santello 2004). Such variety can help restore individuation of biomechanically coupled effectors, in particular the individual fingers of the hand, and also to contribute to negative co-variation of finger forces.

Other brain regions have been suggested as contributors to both unimanual and bimanual multi-element actions. These regions include but are not limited to the basal ganglia (Pollok et al. 2005), cerebellum (Haslinger et al. 2004; Latash 1998; Nair et al. 2003), parietal cortex (DeWeerd et al. 2003; Jeannerod et al. 1995; Kermadi et al. 2000; Nair et al. 2003), prefrontal cortex (Kandel et al. 2000), premotor cortex (Cincotta et al. 2004; DeWeerd et al. 2003; Haslinger et al. 2004), and the supplementary motor area (Deiber et al. 1999; Jancke et al. 2000; Kandel et al. 2000; Kermadi et al. 2000; Nair et al. 2003; Serrien et al. 2002). Unfortunately, information on the role of these structures in motor synergies is fragmented at

best. Nevertheless, it is feasible that motor synergies are organized by distributed neuronal networks involving many of the mentioned structures.

Transitions during a change in the control hierarchy

Previous research by Li et al. (2002) demonstrated the existence of strong interaction effects during tasks that began as unimanual tasks and ended as bimanual tasks. In particular, during the unimanual-to-bimanual transition, quick large amplitude changes in force output of both hands were found. Strong bimanual interactions in isometric tasks have also been found by others (Carson 1995; Ferrand and Jaric 2006; Jaric et al. 2006). Li et al. (2002) have suggested that the strong interaction effects could be due to the minimization of secondary moments of force, that is, moments in the frontal plane produced by the reactive forces and acting on the body (Li et al. 1998, 2001; Zatsiorsky et al. 2000); however, it seems feasible that those effects could also get contribution from changes in the control hierarchy as in the current set of experiments.

Adding a finger-pair to or removing a finger-pair from a set of fingers involved in a constant force production task was associated with poorly reproducible transient changes in the total force that were accompanied by an increase in force variability and a drop in all indices related to force-stabilizing synergies (Fig. 4). Such a drop has been interpreted in two ways in previous studies. One interpretation is that the sudden weakening of the within-a-hand synergy may represent a purposeful destabilization of the total force in order to facilitate its adjustment (Kim et al. 2006; Olafsdottir et al. 2007; Shim et al. 2005b). An alternative interpretation is that the drop in the synergy index might result from the combination of a high rate of force change and timing errors in the forces produced by individual fingers (Goodman et al. 2005). The average delay between the changes in the force produced by a pair of fingers and the changes in the index of force-stabilizing synergy computed for that pair was not significantly different from zero. The large variability of the time delay between changes in ΔV and in the force produced by a finger-pair across subjects has suggested that, at least in some subjects, the change in ΔV reflected a feed-forward control process, which is more in line with the former of the two suggested interpretations.

Concluding comments

The inability of the CNS to organize novel multi-finger force production synergies simultaneously at two levels of a control hierarchy has been confirmed by this experiment, independently of the number of hands used in a task. Further investigation into this phenomenon is needed since these results are in conflict with studies on prehension (Shim et al. 2005a; Zatsiorsky et al. 2003). The development of experiments analyzing novel two-hand prehension are needed in order to reconcile the two seemingly disparate findings.

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

Fig. 2.

An illustration of total force (F_{TOT}), $VarF_{TOT}$ and $\Sigma VarF_i$ profiles from a representative subject. Data averaged over 15 trials are shown. **a** Total force (F_{TOT}), $VarF_{TOT}$, and $\Sigma VarF_i$ produced by all fingers in the task *ADD IM_L to IM_R* . **b** Total force (F_{TOT}), $VarF_{TOT}$, and $\Sigma VarF_i$ produced by all fingers in the task *REMOVE IM_L from $IM_R + IM_L$* . Note that $\Sigma VarF_i > VarF_{TOT}$ in the plots (with the exception of the beginning of the trials). This indicates negative finger force co-variation and the presence of strong task-finger synergies throughout the shown tasks

Fig. 3.

a The measure $\Sigma \text{Var} F_i$ during *Stage-1* and *Stage-2* were averaged within the *ADD* and *REMOVE* conditions across all subjects. **b** Mean $\Delta V_{\text{within-a-pair}}$ indices for *Stage-1* and *Stage-2* under the *ADD* and *REMOVE* instructions are shown. In this figure, the bars show data averaged across subjects for bimanual conditions only. **c** $\Delta V_{\text{within-a-pair}}$ indices averaged across subjects for the *ADD* and *REMOVE* instructions involving finger-pairs IM + RL distributed across either one- or two-hands in *Stage-1*. **d** $\Delta V_{\text{within-a-pair}}$ indices averaged across subjects for the *ADD* and *REMOVE* instructions involving the finger-pairs IM + RL distributed across either one- or two-hands in *Stage-2*. Standard error bars are shown in all panels. Panel **b** shows that within-a-finger pair synergies are absent when two hands are involved in a task. In panel **c**, it is shown that within-a-finger pair synergies are present for *ADD* tasks in *Stage-1* compared to *REMOVE* tasks, independently of the number of hands involved in the tasks. Panel **d** illustrates that within-a-finger pair synergies are present for *REMOVE* tasks in *Stage-2* compared to *ADD* tasks, independently of the number of hands involved in the task.

Fig. 4.

a Mean $\Delta V_{\text{within-a-pair}}$ indices for *Stage-1*, *transient*, and *Stage-2* for the *ADD* and *REMOVE* instructions are shown. The bars show data for bimanual conditions only. **b** Mean $\Delta V_{\text{within-a-pair}}$ indices for *Stage-1*, *transient*, and *Stage-2* in one- and two-hand tasks are shown. **c** Mean $\Delta V_{\text{within-a-pair}}$ indices for the one- and two-hand tasks under the *ADD* and *REMOVE* instructions are shown. **d** Mean $\Delta V_{\text{task-fingers}}$ indices for *Stage-1*, *transient*, and *Stage-2* under the *ADD* and *REMOVE* instructions are shown. The bars show data averaged across all subjects. Standard error bars are shown in all panels. In panel **a**, the destabilization and disappearance of a within-a-finger pair synergies for *ADD* tasks as well as the appearance of within-a-finger pair synergies for *REMOVE* tasks are illustrated. Data in panel **b** reflect weak within-a-finger pair synergies during *Stage-1* followed by the destabilization and disappearance of such synergies in *Stage-2* for both one- and two-hand tasks. In panel **c**, within-a-finger pair synergies are absent in both one- and two-hand tasks under both *ADD* and *REMOVE* instructions. In panel **d**, strong synergies across all fingers explicitly involved in a task are seen in *Stages -1* and *-2* as well as a destabilization of such synergies during the transition between the task stages

Fig. 5.

a An illustration of a two-effector force production task. In the space of elemental variable (forces produced by the effectors) the orientation of "good" and "bad" variability are shown, V_{GOOD} and V_{BAD} . **b** An illustration of a two-hand force production task, in which $V_{GOOD} > V_{BAD}$. Note that variability of individual hand forces (illustrated for one of the hands) reflects both V_{BAD} and V_{GOOD} . **c** An illustration of a one-hand, two-finger force production, in which $V_{GOOD} = V_{BAD}$. Note that V_{BAD} corresponds to the variability in the force produced by the hand (shown in panel c)