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RESEARCH ARTICLE

Force-stabilizing synergies in motor tasks involving two actors

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Abstract We investigated the ability of two persons to produce force-stabilizing synergies in accurate multi-finger force production tasks under visual feedback on the total force only. The subjects produced a time profile of total force (the sum of two hand forces in one-person tasks and the sum of two subject forces in two-person tasks) consisting of a ramp-up, steady-state, and ramp-down segments; the steady-state segment was interrupted in the middle by a quick force pulse. Analyses of the structure of inter-trial finger force variance, motor equivalence, anticipatory synergy adjustments (ASAs), and the unintentional drift of the sharing pattern were performed. The two-person performance was characterized by a dramatically higher amount of inter-trial variance that did not affect total force, higher finger force deviations that did not affect total force (motor equivalent deviations), shorter ASAs, and larger drift of the sharing pattern. The rate of sharing pattern drift correlated with the initial disparity between the forces produced by the two persons (or two hands). The drift accelerated following the quick force pulse. Our observations show that sensory information on the task-specific performance variable is sufficient for the organization of performance-stabilizing synergies. They suggest, however, that two actors are less likely to follow a single optimization criterion as compared to a single performer. The presence of ASAs in the two-person condition might reflect fidgeting by one or both of the subjects. We discuss the characteristics of the drift in the sharing pattern as reflections of different characteristic times of motion within the subspaces that affect and do not affect salient performance variables.

Introduction

All motor actions are based on *redundant* (Bernstein 1967; more precisely, *abundant*, Latash 2012) sets of elements such as muscles, joints, digits, etc. Even a single-muscle action may be viewed as abundant when considered at the level of recruitment of individual motor units. This abundance of elements offers the central nervous system (CNS) an opportunity to organize them into task-specific groups, or *synergies*, which stabilize salient performance variables (Schöner 1995). The stability of motor actions is highly important because of the unpredictable and continuously changing external conditions and internal states of the body.

Quantitative methods to analyze synergies have been developed within the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999). One of these methods compares inter-trial variance of the elemental variables in two subspaces: variance in the UCM subspace (V_{UCM}) does not affect the selected performance variable, while variance in the subspace orthogonal to the UCM (V_{ORT}) leads to changes in that performance variable. When $V_{UCM} > V_{ORT}$, it is concluded that a multi-element synergy is stabilizing that performance variable with respect to which the analysis was performed (reviewed

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in Latash et al. 2002, 2007). Another method of analyzing task stability (Mattos et al. 2011, 2013, 2015) quantifies intra-trial deviations of the system in directions that keep a potentially salient performance variable unchanged (within the UCM for that variable) and in directions that lead to changes in that variable (within the subspace orthogonal to the UCM). Deviations within the UCM are called motor equivalent (ME) because they do not change the performance variable, while deviations orthogonal to it are non-motor equivalent (nME). Large ME deviations during quick actions and reactions have been interpreted as reflections of a system's relatively low stability within the UCM.

Until recently, most studies of synergies within the described framework involved actions performed by one person. Studies of motor coordination in groups involving two or more persons can be divided into two types according to the sort of cooperation subjects were asked to exhibit. Experiments of the first type involved people performing individual motor tasks while watching each other (Schmidt et al. 1990; Fine and Amazeen 2011; Fine et al. 2013), talking to each other (Shockley et al. 2003; Stoffregen et al. 2009), or having haptic contact (van der Wel et al. 2011). Several of those studies have reported that agents in these groups exhibit patterns of behavior similar to those, which would be seen when one person coordinates multiple limbs (Schmidt et al. 1990; Fine and Amazeen 2011; Fine et al. 2013). In particular, stabilization of relative phase during two-limb motion has been reported in both one-person and two-person tasks and explored using a method based on the UCM hypothesis (Black et al. 2007; Riley et al. 2011).

The other type of experimental studies required people to coordinate their action to achieve a common mechanical outcome such as in a virtual lifting task (Knoblich and Jordan 2003; Bosga and Meulenbroek 2007) or the production of a rhythmical pattern of finger force (Masumoto and Inui 2013). These studies produced conflicting results: the former studies reported that two-person actions were less accurate than individual actions, while the latter study reported that coordinated two-person control of force was more accurate than individual actions.

The current study is a comprehensive exploration of multi-finger synergies stabilizing the production of total force in one-person and two-person actions. In particular, we addressed three main issues: first, can force-stabilizing synergies be organized by two motor systems linked only by a visual signal regarding common output? Different schemes have been offered for synergies based on short-latency back-coupling loops (Latash et al. 2005), back-coupling loops from sensory signals (Martin et al. 2009), and optimal feedback control schemes

(Todorov and Jordan 2002). If such synergies can be organized by two CNSs linked by visual information only (Hypothesis 1), this observation would favor one of the two latter schemes, and would also be compatible with reports from earlier studies (Bosga and Meulenbroek 2007; Masumoto and Inui 2013). We used both the synergy index (ΔV, the normalized difference between V_{UCM} and V_{ORT}) and the concept of motor equivalence to address this question.

Second, we wanted to test whether feed-forward synergy adjustments prior to production of a quick force pulse (anticipatory synergy adjustments, ASAs, Olafsdottir et al. 2005; Shim et al. 2005) could be organized by two CNSs linked only by visual feedback on their combined performance and the required timing of the force pulse initiation. While temporal feedback about action of the other person can be used in anticipatory action control (Knoblich and Jordan 2003), no studies have explored whether anticipatory control could be used when feedback was provided only on the joint outcome. Based on the only available study, we hypothesized that ASAs would be similar in two-person and one-person tasks (Hypothesis 2).

Finally, we tested whether the pattern of total force sharing between subjects might drift toward some (potentially optimal) value. In an abundant task, all "solutions" on the UCM are by definition equally able to solve the problem. However, certain preferred patterns of sharing the task among elemental variables have been observed in one-person tasks (Li et al. 1998), and subjects who begin performing a task with a sharing pattern that is different from their preferred pattern tend to drift toward that preferred pattern (Ambike et al. 2015). Individual preferences for certain sharing patterns have been viewed as reflections of an optimization principle (cf. Terekhov et al. 2010). Such drifts are slow, similar in their characteristic times to drifts of force in constant force production tasks seen after the visual feedback has been turned off (Vaillancourt and Russell 2002; Ambike et al. 2015). These phenomena have been interpreted within the UCM framework by assuming a degree of coupling between action components in the UCM and ORT subspaces. We expected to see drifts in the sharing pattern in two-person tasks with rates defined by the initial deviations from an assumed preferred pattern (Hypothesis 3A). We also expected these drifts to be accelerated by a quick action (force pulse)—Hypothesis 3B. Since this action occurs in the ORT sub space, accelerated drift is expected for two reasons: (1) processes within ORT are expected to be faster corresponding to higher stability in that subspace; and (2) a quick motion in ORT is expected to induce a comparably quick motion in UCM due to the assumed coupling between UCM and ORT.
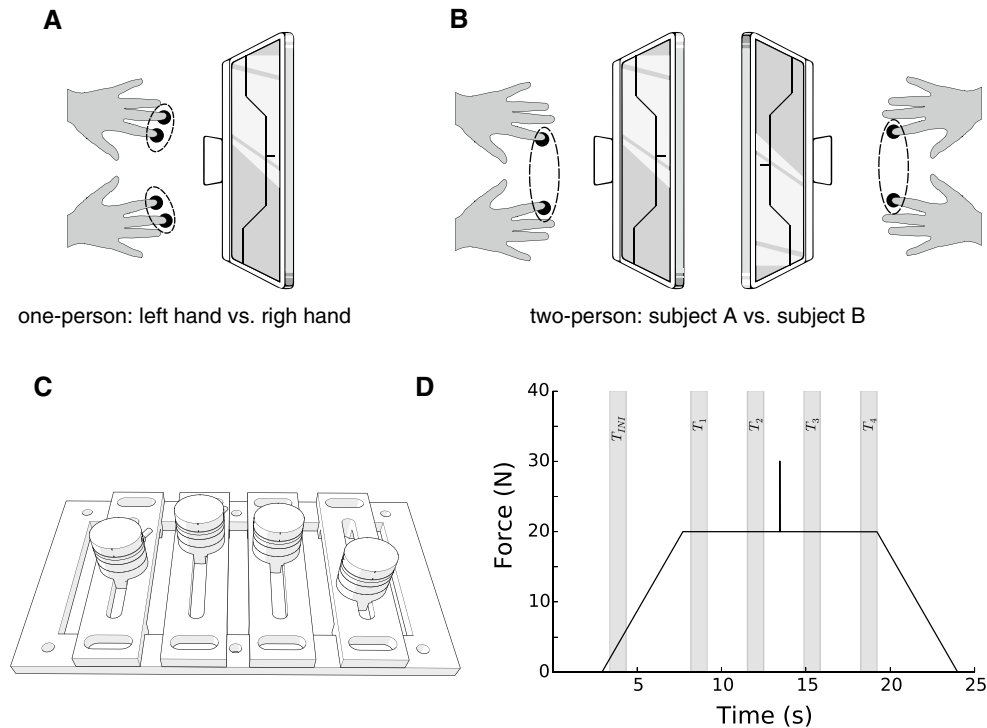
Fig. 1 Schematic representation of the experimental setup for the one-person (**a**) and two-person conditions (**b**). *Solid circles* show force sensors. In the one-person condition, the index and middle finger forces were summed up to represent left and right hand force. In the two-person condition, the forces by the right and left index fingers of individual subjects were summed up. **c** Force sensors within the adjustable panel were fixed to the table in front of each subject. Each sensor was covered with sandpaper (300 grit). **d** The *solid line* represents the force template. The *shaded rectangles* represent five 0.5-s time epochs within which the data were quantified: T_{INI}: 4–4.5 s, T_1: 7.5–8 s, T_2: 11.5–12 s, T_3: 15.5–16 s and T_4: 18.5–19 s

Methods

Subjects

A total of 14 subjects (seven females; 28 ± 5 years of age, 1.71 ± 0.09 m of height, and 69 ± 10.6 kg of mass) took part in the study; these subjects were randomly assigned to form seven pairs. All subjects were healthy without any sensory or motor problems, and none of the subjects reported history of injuries or chronic disorders associated with upper extremities that would interfere with manual tasks. Subjects' hand length from the distal wrist crease to the tip of the longest finger was 18.2 ± 0.7 cm; hand width on the metacarpal level was 8.9 ± 0.6 cm. All subjects were self-reported right handed and gave written informed consent according to procedures approved by the Pennsylvania State University Office of Research Protections.

Apparatus

Four six-component force sensors (Nano-17, ATI Industrial Automation, Apex, NC) were used to measure normal forces generated with fingertips. The force sensors were mounted on adjustable aluminum panels ($140 \times 90 \times 5$ mm, see Fig. 1c) and fixed to a table in front of each subject. The face of each sensor was covered with 300 grit sandpaper to increase friction. Finger force data were digitized at 1000 Hz via the 16-bit data acquisition board (NI PCI-6225, National Instruments, Austin, TX) using a customized LabVIEW program (LabVIEW 2012, National Instruments, Austin, TX), which also displayed real-time feedback to the subjects. Experimental tasks and real-time force data were displayed on two computer screens (22 inch diagonal, 1920×1080 pixels) placed 0.75 m away from each subject.

Experimental procedure

The experiment included two main parts: (1) single-person tasks and (2) two-person tasks. Each subject sat in a chair in front of his or her respective monitor with his or her forearms resting on the table and fingertips placed on the force sensors. In the two-person tasks, the subjects sat facing each other, separated by a partition wall. Subjects could not see each other and verbal communication was not allowed. In both single- and two-person tasks, the

subjects performed the tasks using both hands. In single-person tasks, subjects pressed on sensors with their middle and index fingers of both hands (IM_R and IM_L for the right and left hand, respectively), while during two-person tasks, subjects used only the left and right index fingers (I_RI_{L1} and I_RI_{L2} for subjects 1 and 2, respectively, see Fig. 1, panels a and b). As a result, four fingers were used in every task, regardless of the number of subjects involved. Before each trial, subjects were asked to place their fingers on the sensors and relax; the sensors were zeroed during this time so that only active pressing forces (and not the weight of the fingers) were measured. The order in which single-person and two-person conditions were presented was randomized across subjects.

Force-tracking tasks

In all tasks, the participants were shown a 24-s-long force template consisting of ramp-up (2–7 s), steady-state (7–19 s), and ramp-down (19–24 s) phases (Fig. 1d). The steady-state level was set at 20 N, which was a comfortable force level for all subjects and subject pairs. During the data collection, the total force (F_{TOT}) was calculated as the sum of the four instructed finger forces and displayed to the involved subject(s) as a small red cursor. Subjects were required to press naturally with their fingers and accurately track the force template shown on the screens with the small red cursor. Before each session, subjects were given detailed instructions followed by five practice trials. Each condition was repeated 25 times with 30-s rest breaks to minimize effects of fatigue.

In the middle of the steady-state phase of the template ($t_0 = 13$ s), a vertical line was drawn; subjects were instructed to generate a quick pulse of force when the red cursor reached the vertical line. The magnitude of F_{TOT} during the discrete quick force pulse was not specified, but the cursor had to move beyond the upper edge of the screen, corresponding to peak F_{TOT} of >35 N. We purposefully avoided putting an explicit force target for the pulse because the pulse was only intended to introduce a quick, self-generated perturbation into the steady-state force production task. After the quick force pulse, subjects returned to the steady-state force level as quickly as possible and continued to track the force template.

Maximal voluntary contraction (MVC) tasks

During the MVC task, subjects were required to produce maximum force with the four instructed fingers pressing together for 3 s. The MVC trials were repeated three times with 30-s rest periods between trials, and the data from the trial with highest MVC values were selected. To minimize the effects of fatigue from the MVC trials on performance during the experimental task, the MVC trials were performed at the end of data collection. These MVC values were later used to determine whether strength differences between the subjects forming a pair might have defined their relative contributions to the two-person task.

Data analysis

Prior to the data analysis, finger force data were smoothed with a fourth-order zero-lag Butterworth filter with a 10-Hz cutoff frequency. All data were processed off-line using a customized MATLAB (MATLAB R2011a; The Math-Works Inc, Natick, MA) program.

For the one-person trials, total force (F_{TOT}) was defined as the sum of forces produced by the *M* and *I* fingers of each hand. Similarly, for the two-person trials, F_{TOT} was defined as forces by all four involved *I* fingers.

Synergy analysis (UCM-based analysis)

We quantified the F_{TOT}-stabilizing synergies using the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999). This hypothesis assumes that elements in a redundant system (hand forces or subject forces in different analyses of the current study) are organized by the nervous system into two subspaces such that changes of elemental variables within one subspace (the "uncontrolled manifold" or UCM) do not precipitate changes in a performance variable (F_{TOT} produced by the elemental variables in our study), while changes within the other subspace (ORT; orthogonal to the UCM) directly affect the performance.

Detailed descriptions of this analysis can be found in earlier publications (Latash et al. 2001; Scholz et al. 2002). Briefly: the UCM was computed as the null-space of the Jacobian matrix $J = [1, 1]$ mapping small changes in individual elemental forces (hand forces in one-person tasks and subject forces in two-person tasks) onto changes in F_{TOT}. The UCM-based analysis quantifies inter-trials variance within the UCM and ORT subspaces (V_{UCM} and V_{ORT}, respectively). An index of synergy (ΔV) was computed as $\Delta V = (V_{UCM} - V_{ORT})/(V_{TOT})$, where V_{TOT} is total variance and every variance index is normalized by the number of degrees of freedom of the corresponding spaces. Positive values of ΔV indicate a force-stabilizing synergy (cf. Latash et al. 2001; Scholz et al. 2002). Since the method of computation of ΔV limits its values to the range bounded by -2 (all variance is V_{ORT}) and $+2$ (all variance is V_{UCM}), ΔV distributions were expected to deviate from the normal distribution. Therefore, prior to further statistical analysis, ΔV values were transformed using Fisher's z-transform, resulting in an index ΔV_Z. Four 0.5-s time epochs were selected from the steady-state phase of the template and

used to compute the three variance indices (V_{UCM}, V_{ORT} and ΔV): T_1: 7.5–8 s, T_2: 11.5–12 s, T_3: 15.5–6 s, and T_4: 18.5–19 s (see Fig. 1d).

Task performance error

Task performance was assessed by root-mean-square error (RMSE):

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^{n} \Delta F_i^2}{n}} \tag{1}$$

where ΔF is the difference between the force template value and F_{TOT}, and n is sample number. RMSE was computed over the four time epochs: T_1, T_2, T_3, and T_4.

Anticipatory synergy adjustment

Anticipatory synergy adjustments (ASAs) represent a drop in the synergy index seen in anticipation of the force pulse initiation (Olafsdottir et al. 2005). The time of ASA initiation (T_{ASA}) was identified as the time when ΔV_Z dropped two standard deviations below its average steady-state value quantified between 1.5 and 0.5 s before the onset of the quick force pulse. Negative values of T_{ASA} indicate that ΔV_Z dropped before the force pulse initiation. Additionally, the magnitude of synergy index change during the ASA ($\Delta\Delta V_{Z,ASA}$) was quantified as the difference between ΔV_Z at steady-state and at t_0, with positive values indicating a drop in ΔV_Z. Since changes in the index of synergy ΔV_Z can reflect changes in either V_{UCM} or V_{ORT} or both, we also investigated the changes of variance in each subspace prior to t_0.

Sharing pattern drift

Analysis of *sharing* depended on the experimental conditions: in the single-person trials, the magnitudes of force produced by the subject's left and right hand were compared; for the two-person trials, the magnitudes of force produced by each subject were compared. We defined the relative contribution of elemental variables (hand forces or subject forces) as the sharing pattern (SP), calculated as:

$$\text{SP} = \frac{f_1}{F_{TOT}} \times 100\ \% \tag{2}$$

with f_1 representing either the IM_L force (one-person tasks) or $I_R I_{L1}$ force (two-person tasks). SP = 50 % indicates a perfectly equal sharing of the task between the hands or between the subjects.

Two-person trials were typically associated with obvious SP changes during the steady-state phase of the task (typical time profiles are shown in Fig. 2b). To explore

these behaviors, for each trial, SP drift during the steady-state force production phase was assessed with the least-squares linear regression. To avoid possible effects of the voluntary force pulse at t_0, we applied the linear regression only to the SP values before t_0 (from 7.5 to 12 s of the task). To explore whether the SP drift reflected possible early deviations of the SP from some preferred value, we ran Pearson's correlation analysis to analyze if the rate of SP drift (β_1) was related to the initial value of SP (β_0): $SP(t) = \beta_0 + \beta_1 t$.

It was also possible that the strength difference between subjects forming a pair defined their relative contribution to the task reflected in SP. Therefore, we used Pearson's correlation analysis to investigate if relative subject's contribution to F_{TOT} in two-person tasks was related to strength difference between these subjects. The averaged-across-trials SP values from the early part of the steady-state (T_1) of each subject pair were correlated with the differences of the subjects' MVC values.

We also investigated the possibility that force sharing between hands (single-person condition) or subjects (two-person condition) during the early stage of the steady-state was a consequence of force sharing developed from the trial initiation—immediately after the force onset. For each subject and subject pair, we averaged across trials SP within the initial 0.5 s of the trial (T_{INI}: 2.5–3 s of the task, see Fig. 1d) and correlated these values with averaged-across-trials SP in epoch T_1.

Motor equivalence analysis

This analysis explored the degree to which changes in elemental variables over the trial duration were coordinated to keep F_{TOT} unchanged. This analysis of *motor equivalence* quantifies amount of the within-trial displacement within the UCM and ORT subspaces (Mattos et al. 2011, 2015). The motor equivalence analysis was performed for each trial separately. The analysis was performed in three steps. First, for each steady-state epoch (T_1, T_2, T_3, and T_4.), we computed averaged force values, $\bar{f}$, produced by the elemental variables: hand forces for one-person trials and subject forces for two-person trials. Then, we computed the force difference vectors, $\Delta\bar{f}$, between consecutive epochs T_1–T_2, T_2–T_3, and T_3–T_4. Finally, we projected $\Delta\bar{f}$ onto the null-space and orthogonal subspace of $\mathbf{J}$. The null-space component of $\Delta\bar{f}$ does not affect F_{TOT} and is called motor equivalent (ME). In contrast, the orthogonal component of $\Delta\bar{f}$ does affect F_{TOT} and is called non-motor equivalent (nME). Since the dimensionality of both UCM and ORT spaces was the same (equal to one), it was unnecessary to normalize the ME and nME further. For further statistical analysis, ME and nME component magnitudes were averaged across trials for each subject or pair.
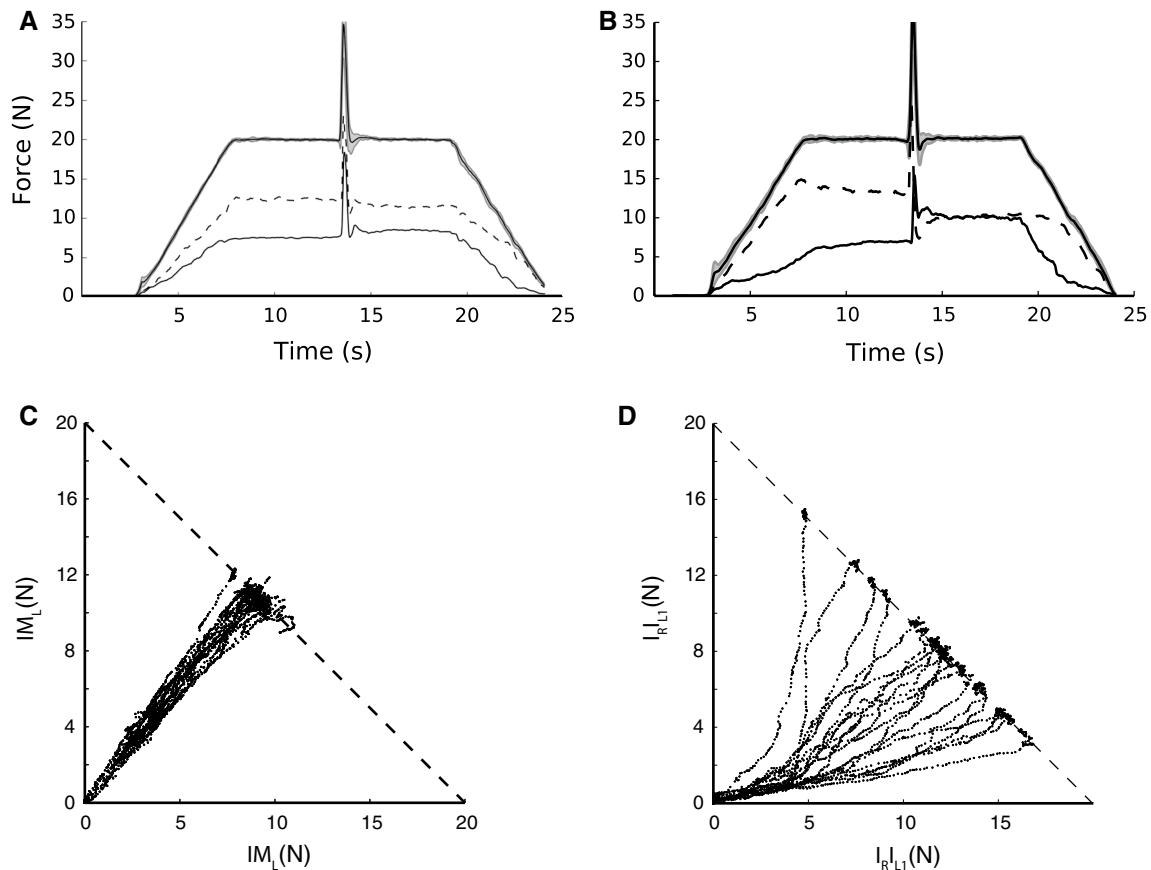
Fig. 2 Typical trials for the one-person (**a**, **c**) and two-person conditions (**b**, **d**). **a** and **b** Averaged-across-trial total force with standard errors (*shaded area*). *Dashed* and *solid lines* represent hand forces (one-person condition, **a**) and subject forces (two-person condition, **b**).

c and **d** show trajectories in the force space over the first 8 s of the task (including the ramp-up and initial phase of the steady state); each trajectory represents an individual trial

Statistical analysis

All descriptive statistics reported in the text and figures represent means and standard errors unless otherwise stated. For each subject, RMSE values were averaged across repetitions. A modified *t* test for unequal sample sizes was used to analyze differences in RMSE, T_{ASA}, and $\Delta\Delta V_{Z, ASA}$ between single-person and two-person conditions. Pearson's correlation coefficients were transformed using Fisher's formula before averaging.

Repeated-measures ANOVA were used to test the effects of *Time* (four levels: T_1, T_2, T_3, and T_4) and *Condition* (between-subjects factor, two level: single-person and two-person) on RMS_{ERROR}, V_{UCM}, V_{ORT}, and ΔV_Z. Repeated-measures ANOVA was also used to test the effect of *Epoch-Difference* (three levels: T_1–T_2, T_2–T_3, and T_3–T_4) and *Condition* on ME and nME indices. We used type III sums of squares ANOVA to account for unbalanced number of observations in *Condition* factor. Greenhouse–Geisser correction was used when the

assumption of sphericity was violated. Simple effects post-hoc tests with Sidak adjustments were used in the analysis of interactions effects. All statistical tests were performed with SPSS software (SPSS 19.0; IBM Inc, Armonk, NY), and a significance level of $p = 0.05$ was selected.

Results

Task performance

Overall, in all conditions, subjects performed the force-tracking task successfully. Subjects did not report any signs of fatigue or discomfort.

Figure 2 shows a typical trial for the single-person (panel a) and two-person conditions (panel b). Task performance in the two conditions was similar: subjects in both conditions were able to accurately track the required target force (F_{TOT} shown as the thick solid line with standard error

Fig. 3 Results of the uncontrolled manifold analysis. The *left* and *right* columns show results for the one-person and two-person conditions, respectively. *Panels represent*: *top*—V_{UCM}, *middle*—V_{ORT}, and *bottom*—ΔV_Z. Averaged values across subjects with *standard error bars* are shown for each steady-state time epoch (T_1, T_2, T_3, and T_4)
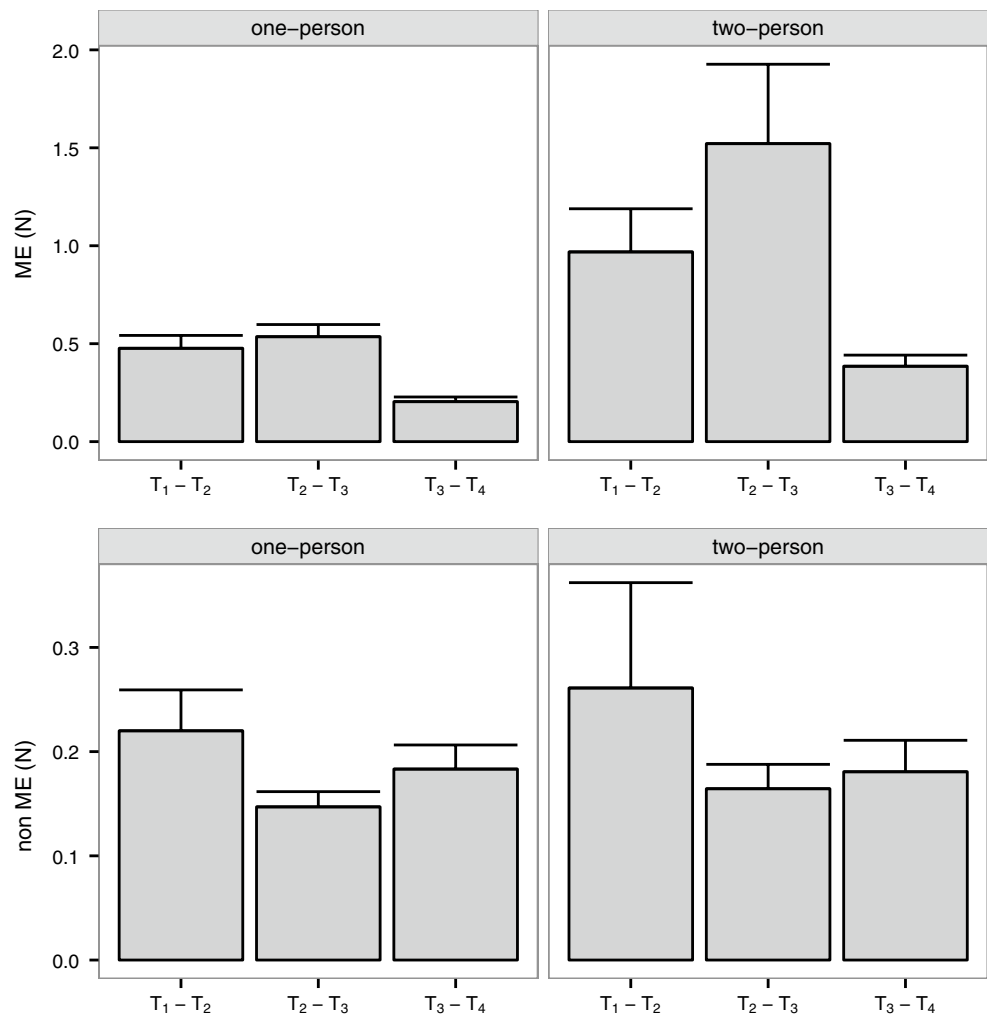
shade). In particular, subjects were able to quickly return to the required force target after the quick force pulse produced at t_0. In both conditions, the relative contribution to F_{TOT} by subjects or hands was regularly observed to change during the steady-state phase. These changes in sharing pattern were accelerated by the voluntary force pulse and were more apparent in the two-person condition. This can be seen in panels a and b of Fig. 2 where the dashed and solid thin lines represent individual hand (one-person condition, panel a) and subject (two-person condition, panel b) forces. RMS_{ERROR} values were similarly small for the single-person and two-person conditions, and over the four steady-state time epochs: 0.48 ± 0.12 N over T_1, 0.19 ± 0.02 N over T_2, 0.21 ± 0.04 N over T_3, and 0.41 ± 0.11 N over T_4 for the single-person condition; and 0.26 ± 0.18 N over T_1, 0.13 ± 0.03 N over T_2, 0.29 ± 0.06 N over T_3 and 0.27 ± 0.16 N over T_4 for the two-person condition. There were no significant main effects of *Time* or *Condition* ($p = 0.12$ and $p = 0.48$, respectively), and no interaction ($p = 0.32$).

Analysis of synergies (UCM-based analysis)

To quantify synergies that stabilized F_{TOT}, we analyzed the structure of inter-trial variance in hand forces (one-person) and subject forces (two-person) in four time epochs (T_1, T_2, T_3, and T_4) during the steady force production segment of the task. The results are summarized in Fig. 3. F_{TOT}-stabilizing synergies were observed across all time epochs and conditions: V_{ORT} values were substantially smaller than V_{UCM}. Both V_{ORT} and V_{UCM} values were largest during the initial phase of the steady-state (time epoch T_1) in both one-person and two-person tasks.

There was a striking difference in the V_{UCM} values between the one-person and two-person conditions. This difference is evident from visual inspection of the spread of the data along the UCM in panels c and d of Fig. 2: on average, V_{UCM} was more than an order of magnitude higher during the two-person condition compared to the one-person condition (9.03 ± 0.72 N^2 vs. 0.78 ± 0.5 N^2, respectively). Over the steady-state portion of the task, V_{UCM}

showed a substantial decrease in both conditions, but the decrease was greater in the two-person condition (Fig. 3, top panel).

Statistical analysis confirmed these results: V_{UCM} was significantly higher for the two-person condition ($F_{1,19} = 87.9$, $p < 0.001$), and there was a significant effect of *Time* ($F_{1.6,31.6} = 155.2$, $p < 0.001$) on V_{UCM}. There was also a significant *Time × Condition* interaction ($F_{1.6,31.6} = 129.49$, $p < 0.001$). The simple effects post-hoc test revealed that V_{UCM} values at each *Condition* level were significantly different from one another across all *Time* levels ($p < 0.001$), while V_{UCM} significantly decreased with time in the two-person condition only ($p < 0.001$). The component of variance affecting the task performance (V_{ORT}) was much smaller than V_{UCM} for both one-person and two-person tasks ($0.54 \, N^2 \pm 0.26$ vs. $0.89 \, N^2 \pm 0.36$, respectively); statistical analysis showed no significant effects on V_{ORT}.

Index of synergy (ΔV_Z) reflected results described above (i.e., $V_{UCM} > V_{ORT}$). ΔV_Z values were positive for both one-person and two-person conditions and for all time epochs. The substantial increase in V_{UCM} for the two-person condition resulted in higher ΔV_Z values: in two-person conditions, ΔV_Z was considerably larger than in the one-person conditions ($\Delta V_Z = 2.7 \pm 0.18$ vs. 1.61 ± 0.12, for two-person and single-person conditions, respectively).

ANOVA confirmed significant main effects of *Time* ($F_{3,57} = 9.48$, $p < 0.001$) and *Condition* ($F_{1,19} = 24.15$, $p < 0.001$) on ΔV_Z. Post-hoc tests revealed that the highest ΔV_Z values were seen during T_2 ($p < 0.05$). There was no significant interaction.

Motor equivalence

The described above within-trial SP drifts were accompanied by only minor changes in F_{TOT} (see panels a and b of Fig. 2), which indicates that the force deviations were mostly within the UCM subspace. This observation was supported by the motor equivalence (ME) analysis. For every time epoch and for both conditions, ME values were higher than nME values (see Fig. 4). In addition, ME displacement was more than twice as large in trials performed in pairs compared to those in the one-person condition ($0.96 \, N \pm 0.11$ vs. $0.41 \, N \pm 0.08$, respectively).

For both task conditions, the largest ME displacements occurred between the steady state before the force pulse initiation (t_0) and the time interval following the force pulse (T_2–T_3) and were more noticeable in tasks performed in pairs ($1.52 \, N \pm 0.23$ vs. $0.53 \, N \pm 0.16$, for two-person and one-person conditions, respectively). An example of such behavior can be seen in panes A and B of Fig. 2: after the force pulse in the middle of the trial (at 13 s), the contribution of hand forces for the one-person condition and

subject forces for the two-person condition changed, but the change was more evident in the two-person condition. In both conditions, the lowest ME displacement was seen between epochs T_3 and T_4, that could correspond to smaller SP drifts at the end of the steady state ($0.38 \, N \pm 0.42$ and $0.2 \, N \pm 0.03$, for the two-person and one-person conditions, respectively).

Non-motor equivalent (nME) displacements were of similar (small) magnitude in both one-person and two-person conditions ($0.2 \, N \pm 0.03$ and $0.18 \, N \pm 0.02$, across all time epochs, respectively). Average nME displacement was largest in the early portion (T_1–T_2) of the steady state confirming that the rapid switch from ramp-up to the steady-state task affected the performance accuracy.

Statistical analysis confirmed these results. There was a significant effect of *Epoch-Difference* ($F_{(1.4, 26.2)} = 17.74$, $p < 0.001$), *Condition* ($F(1,19) = 15.52$, $p = 0.001$) and *Epoch-Difference × Condition* interaction ($F_{(1.4, 26.2)} = 5.31$, $p < 0.05$) on ME. The simple effects post-hoc test showed that at each level of *Epoch-Difference* ME was significantly higher for the two-person condition. In the two-person condition, ME in both T_1–T_2 and T_2–T_3 was significantly different from T_3 to T_4, but in the one-person condition, only ME in T_2–T_3 was significantly different from T_3 to T_4. ANOVA on nME showed no significant effects.

Anticipatory synergy adjustments

There was typically a drop of ΔV_Z prior to the voluntary force pulse initiation under both one-person and two-person conditions anticipatory synergy adjustments (ASAs; panels a and b of Fig. 5). There were no visible changes in F_{TOT} during ASAs in either condition (see panels c and d of Fig. 5). There was, however, a large difference in the time of ASA initiation (T_{ASA}) between the two conditions. On average, ASAs in the one-person condition started as much as 180 ms earlier than in the two-person condition ($-354 \, ms \pm 45.6$ vs. $-174 \, ms \pm 51.9$, respectively; $p < 0.05$). Even though ASAs began much earlier in the one-person condition, the magnitude of the ΔV_Z drop over the ASA ($\Delta \Delta V_{Z,ASA}$) was not significantly different between the two condition (0.86 ± 0.15 vs. 0.55 ± 0.12, for the one-person and two-person conditions, respectively).

Separate analysis of V_{ORT} showed similar results. The increase in V_{ORT} started about 170 ms earlier in the one-person condition compared to the two-person condition (-332.4 ± 43.8 ms vs. -159.4 ± 54.2 ms, respectively; $p < 0.05$). However, the magnitude of V_{ORT} change did not differ significantly between the conditions ($-0.37 \, N^2 \pm 0.15$ vs. $-0.11 \, N^2 \pm 0.07$; the negative values indicate that V_{ORT} increased during ASA). No consistent change in V_{UCM} during ASA was observed.

Fig. 4 Results of the motor equivalence analysis for the one-person (*left panels*) and two-person (*right panels*) conditions. *Panels* show averaged-across-subjects motor equivalent (ME, *top*) and non-motor equivalent (nME, *bottom*) displacements with standard error bars between time epochs (T_1–T_2, T_2–T_3, and T_3–T_4)
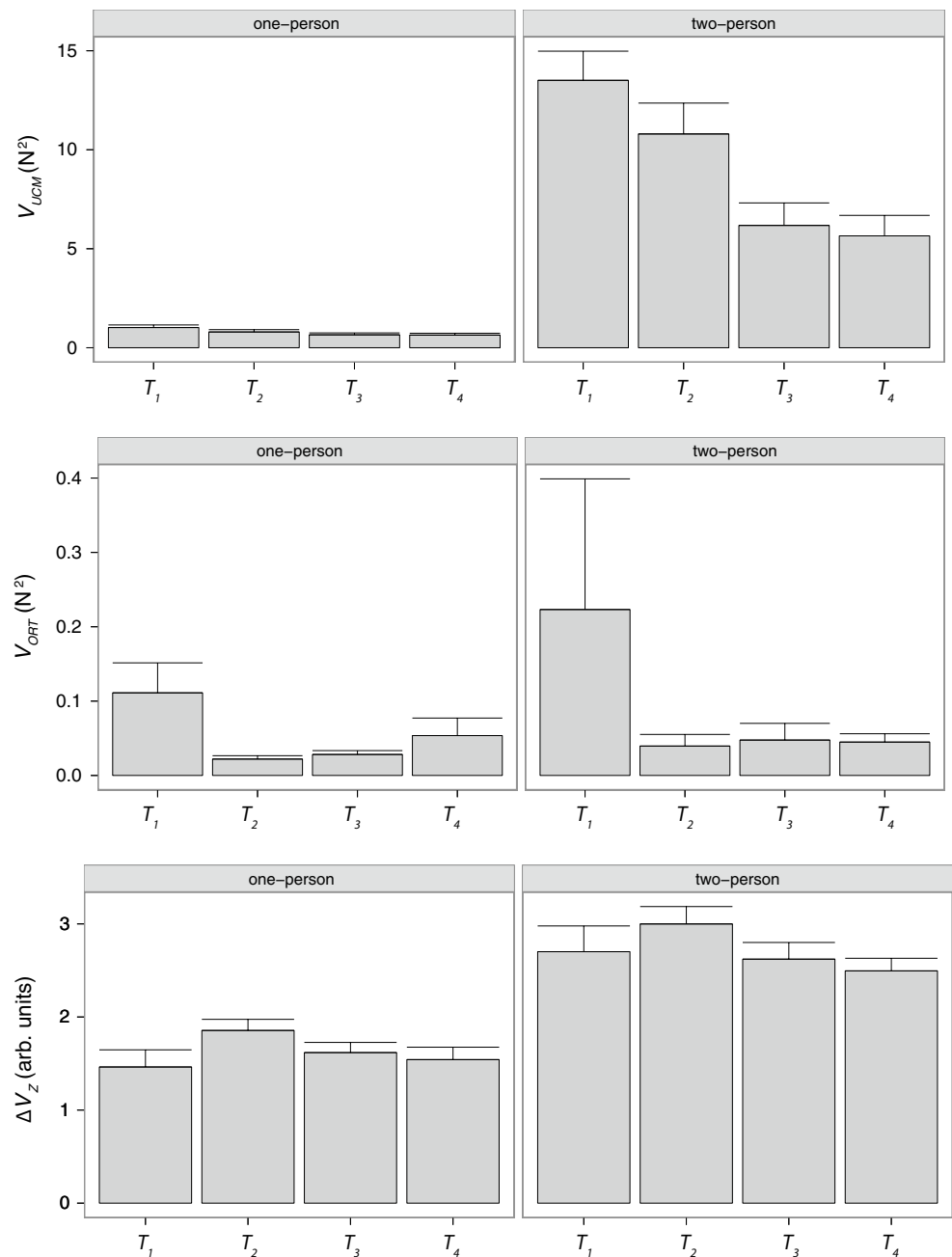
Sharing pattern drift

The relative contribution of elemental variables (sharing pattern—SP—of hand or subject forces, see "Methods") varied from trial to trial in both conditions; however, two-person trials were associated with notably higher variability in SP values across trials. The typical one-person and two-person behaviors are represented in Fig. 2c, d. Panels c and d show dotted trajectories in the force space from the first 8 s of the force-tracking task (including ramp-up and the initial phase of the steady state), and each trajectory represents an individual trial. In the two-person condition, the contribution of elemental variables varied much more across trials, than in the one-person condition. We also observed within-trial drifts of SP during the F_{TOT} steady states. Panels a and b of Fig. 2 show that during the steady-state (constant F_{TOT} values) the relative contribution of individual forces changed with time (SP drift), and two-person trials were usually associated with larger SP drifts.

We used Pearson's correlation analysis to explore whether the relative contribution of individual subjects in the two-person task at the early steady-state (T_1) was defined by the strength differences between subjects
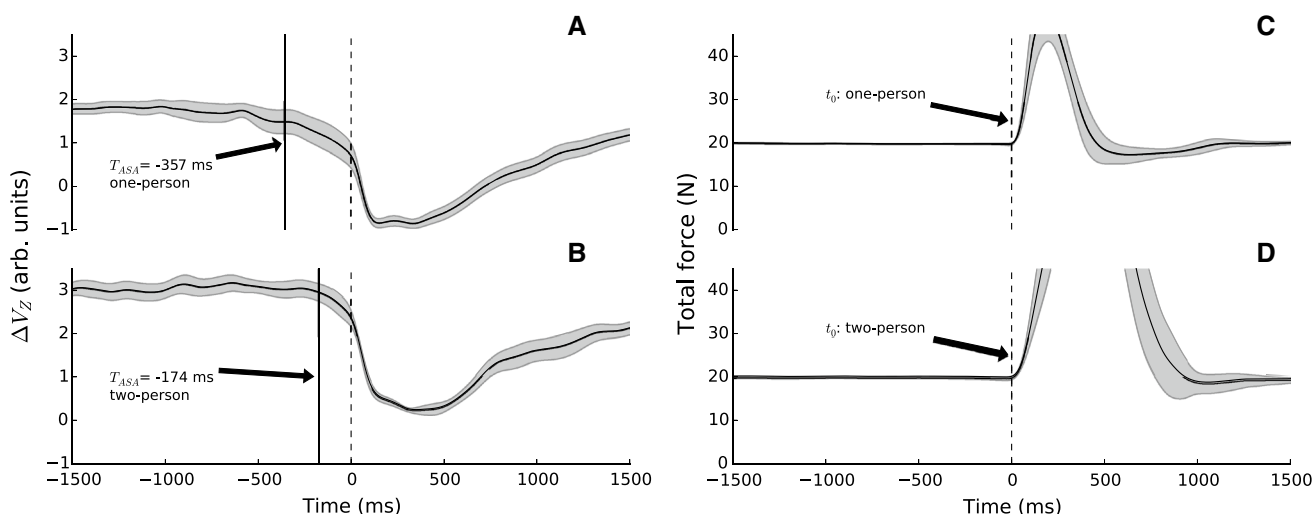
Fig. 5 *Left* Averaged-across-subjects ΔV_Z trajectories with shaded *standard error bars* for the one-person (*top panel* **a**) and two-person (*bottom panel* **b**) conditions. The time of quick force pulse initiation (t_0) is marked with the *vertical dashed line*. In both conditions, there was a noticeable drop in ΔV_Z that started before t_0. Note, however, that the ΔV_Z drop (anticipatory synergy adjustment, ASA) started earlier for the one-person condition (ASA initiation time, T_{ASA}, is indicated with the *vertical solid lines*). *Right* Typical total force trajectories from single-person (*top panel*, **c**) and two-person (*bottom panel*, **d**) conditions, averaged across trials with *standard error shades*. Note that averaged total force showed no visible changes during the ASA

constituting the pair. Results showed no significant correlation between SP during T_1 and MVC differences between subjects forming these pairs ($r = 0.23$, $p = 0.61$). We also investigated the possibility that the relative contribution of individual forces during the early steady-state was defined earlier, in the initial phase of force production (T_{INI}). The correlation analysis between SP values during T_{INI} and T_1 was performed for both one-person and two-person conditions. Only in the two-person condition was a subject's contribution to the task in the early steady state (T_1) related to the SP developed immediately after the task started. The correlation between SP values in T_{INI} and T_1 was significant for the two-person but not single-person conditions ($r = 0.86$, $p < 0.01$, and $r = 0.27$, $p = 0.33$, respectively).

We frequently observed higher rates of SP drift in trials with highly unbalanced initial SP values in T_1. Nine of the 14 subjects in the one-person condition and 5 out of the 7 pairs showed a significant correlation between the rate of SP change (β_1) and initial SP value (β_0) (see "Methods" and Table 1). The average correlation coefficients (r-values) of the significant correlations were -0.67 and -0.69 for the one-person and two-person conditions, respectively. In all cases, including the non-significant ones, r-values were negative ($p < 0.05$ according to the sign test), showing that, when SP at the beginning of the steady-state (in T_1) were further away from equal sharing (50 %), the SP values drifted at a higher rate toward more equal contribution later in the task.

Table 1 Results of the Pearson correlation analysis between the rate of sharing pattern change (β_1) and initial values of the sharing pattern (β_0)

Subject/pair no.	Condition	
	One-person	Two-person
1	**−0.71**	**−0.72**
2	**−0.68**	**−0.59**
3	−0.30	−0.24
4	**−0.81**	−0.36
5	**−0.72**	**−0.69**
6	−0.10	**−0.81**
7	**−0.44**	**−0.61**
8	**−0.55**	–
9	−0.13	–
10	−0.38	–
11	**−0.83**	–
12	**−0.65**	–
13	−0.22	–
14	**−0.55**	–

* Values in bold indicate significant correlations at $p < 0.05$

Discussion

All three of the specific hypotheses have been confirmed, at least partly. To test Hypothesis 1 that two-person tasks can show force-stabilizing synergies, we analyzed task performance using two methods based on the UCM hypothesis

(Scholz and Schöner 1999). First, we compared the variance components that affected total force (V_{ORT}) and that did not affect total force (V_{UCM}). Second, system displacements in directions that do (motor equivalent, ME) and do not affect total force production (non-motor equivalent, nME) were quantified. Notably, V_{UCM} was much higher in the two-person condition than in the one-person condition, while V_{ORT} was not statistically different between the two conditions. Similarly, ME displacement was larger in the two-person task than in the one-person task. Both of these results suggest that synergies can be organized by two central nervous systems linked by visual feedback.

We expected to see similar anticipatory synergy adjustments (ASAs, Olafsdottir et al. 2005) prior to the intentionally produced force pulse in the one- and two-person conditions (Hypothesis 2). The data provided partial support for this hypothesis. While ASAs were seen in both conditions, the ASA onset was delayed (closer to the time of the force pulse initiation) in the two-person condition compared to the one-person condition.

To test Hypothesis-3, we quantified the sharing pattern across several time intervals. In the one-person condition, the initial sharing pattern drifted toward equal contribution of elements to total force, this drift happened over a relatively long period of time and was positively related to the initial imbalance of sharing between hands. A similar drift was observed in the two-person condition, although the initial sharing in those tasks was more variable than in the one-person condition. As predicted by Hypothesis-3B, when subjects produced a quick force pulse, the sharing drift was accelerated in both one- and two-person conditions.

On the origin of synergies

The term *synergy* is used in motor control and other fields with multiple meanings (Latash 2008). Classically, in clinical terminology, *synergies* are involuntary and stereotypical muscle activation patterns, often seen in stroke patients, which interfere with voluntary movements (Bobath 1978; De Wald et al. 1995). In motor control, *synergy* has most often been used to denote groups of variables, which scale together across the parameters (such as duration, amplitude, etc.) of a motor task (d'Avella et al. 2003; Ivanenko et al. 2004; Ting and Macpherson 2005). Such *synergies* have been viewed as part of a solution to the problem of motor redundancy in the tradition of Bernstein (1967): grouping variables allows reducing the redundancy compared to a situation when each variable is manipulated independently.

Within the framework of the UCM hypothesis, a *synergy* is a neural organization of elemental variables which serves to *stabilize* a salient performance variable (Latash et al. 2007). Within this framework, performance of a motor task by an abundant system can be characterized by *sharing* (average across trials contributions of individual elemental variables) and inter-trial *co-variation* stabilizing salient performance variables. Optimization approaches have been used to interpret experimentally observed sharing patterns (reviewed in Prilutsky and Zatsiorsky 2002), and more recently a method to identify cost functions based on experimental observations has been offered (analytical inverse optimization, ANIO, Terekhov et al. 2010). Analysis of inter-trial variance components, V_{UCM} and V_{ORT}, has been used to quantify the co-variation feature of synergies.

This understanding of synergies is close in spirit to two notions: those of a structural unit (Gelfand and Tsetlin 1966) and of a coordinative structure (Kugler et al. 1980). Structural units were assumed to represent groups of elements organized in a flexible, task-specific way, which is an important feature of synergies. Unlike synergies, however, this notion was not explicitly linked to stability of performance. Coordinative structures were viewed as consequences of perception–action coupling leading to patterned behavior produced by groups of elements. In an illustration from Kugler and Turvey (1987): when termites build a mound, they seem to act individually but their acts are modified due to changes in the actual state of the mound. Since the actual state of the mound reflects accumulated effects of actions of all the termites, each termite in fact coordinates its actions with those who have already contributed to the building process. As such, coordinative structure is a notion very similar to synergy. Synergy, however, may be a broader notion: synergies can be built on feed-forward processes (Goodman and Latash 2006) or back-coupling loops within the central nervous system (Latash et al. 2005), and without coupling from sensory receptors.

Following an optimization principle is not readily compatible with large amounts of V_{UCM} (Park et al. 2010). When a system follows an optimization principle in force production, it is expected to produce a relatively stereotypical sharing pattern with minimal variability about the optimal solution. In contrast, large magnitudes of V_{UCM} imply highly variable sharing patterns being used to perform the same task, which naturally correspond to large deviations from any single optimal sharing pattern. In our experiment, the initial steady-state sharing in two-person conditions varied broadly—resulting in much larger V_{UCM} compared to the one-person conditions (Figs. 2, 3). These observations suggest that the visual feedback on the performance variable (F_{TOT}) was adequate to produce strong synergies stabilizing F_{TOT}, but it led to major deviations from any optimality criterion assuming that such a criterion existed. In other words, two persons performed less optimally but with stronger synergies compared to single persons.

The wide range of sharing patterns in the two-person condition could be related to the development of those sharing patterns during the early phase of the trials. At the beginning of each trial, subjects were asked to produce isometric finger forces to follow a ramp profile. Subjects only received feedback on the sum of their (and their partner's) finger forces, and it happened that they started each trial with a wide range of relative force magnitudes. This could lock them into a particular sharing pattern, which remained relatively invariant during the initial phase of each trail (see Fig. 2). Since a subject could not predict the contribution from his or her partner, the initial sharing varied across trials resulting in the larger inter-trial V_{UCM} in the two-person condition. This possibility is corroborated by the significant correlation between the initial and steady-state sharing patterns in the two-person condition but not in the one-person condition.

The faster drift of the sharing pattern to a more equal distribution of forces between the two actors can be seen as motion toward an optimal solution (Fig. 5) possibly influenced by the increased disparity with the optimal sharing pattern. Note, however, that even at the end of the trial, V_{UCM} for the two-person condition remained much larger than for the one-person condition.

Several theoretical schemes have been suggested for synergies based on ideas of optimal feedback control (Todorov and Jordan 2002), action of short-latency feedback within the CNS (back-coupling, Latash et al. 2005), and action of feedback from sensory receptors (Martin et al. 2009). The very strong synergies observed in the two-person condition show that sensory information on the salient performance variable (F_{TOT}) is sufficient for the creation of synergies. Clearly, no short-latency feedback could be used by the two subjects because of the involvement of two separate CNSs. Earlier studies, however, suggested that synergies could emerge at time scales not compatible with action of sensory-mediated feedbacks. These observations led to the creation of the aforementioned model based on within-the-CNS back-coupling and also to a model of a purely feed-forward mechanism for producing synergies (Goodman and Latash 2006). Taken together, these observations suggest that synergies can be created based on different mechanisms, feed-forward and feedback, involving and not involving signals from sensory receptors.

Could the mirror-neuron system (reviewed in Rizzolatti and Fogassi 2014) be used in two-person synergies? This is an attractive idea which is completely speculative at this time and deserves special exploration. One way to study it could be using two-person tasks with very different sets of effectors, thereby discouraging involvement of the mirror-neuron system. For example, a study could involve action by one subject's foot and another subject's hand, without the subjects' knowledge of the asymmetry.

Unintentional drifts in performance and sharing

Unintentional drifts in performance have been documented in several studies involving accurate force production tasks (Vaillancourt et al. 2001; Shapkova et al. 2008; Ambike et al. 2015). Those studies have shown that removing visual feedback results in a slow decrease in force production. Moreover, when a particular sharing pattern was prescribed in a two-finger accurate force production task using visual feedback and the feedback was turned off, the sharing showed a drift toward a more equal force distribution between the two fingers with a time constant similar to that of the F_{TOT} drift—the exponential fitting of the data suggested time constants on the order of 15 s (Ambike et al. 2015). In our experiment, visual feedback on F_{TOT} was always available to the subjects, while no feedback on the sharing pattern was offered. It is therefore unsurprising that F_{TOT} drift was not observed, but a slow sharing drift was seen.

A drift in sharing occurs by definition within the UCM. The speed of this drift should correspond to the low stability within the UCM (reflected in the large V_{UCM} and ME indices). Across both one-person and two-person conditions, all subjects showed larger sharing drift magnitudes for trials characterized by a larger imbalance of forces between the two effectors (two hands in the one-person conditions and two subjects in the two-person conditions). This suggests that the rate of the sharing drift could be defined by the initial deviation of the sharing from some optimal value (cf. the larger rate of sharing drift for larger initial sharing difference in Ambike et al. 2015). These hypothetical optimal values could differ across subjects and subject pairs. However, the described dependence of the sharing drift on the initial sharing imbalance strongly suggests that optimal sharing values exist across conditions including the two-person conditions. So, the conclusion that two-person conditions poorly reflect optimality should be qualified: an optimality principle (a cost function) may exist in two-person interactions, but it is not followed as consistently as in one-person tasks.

Another important result is the accelerated sharing drift following the force pulse production. A force pulse must occur in the ORT space, which is characterized by higher stability and faster processes with time constants on the order of 1 s, as shown in studies with unintentional force and position drift following external perturbations applied to the system (Wilhelm et al. 2013; Zhou et al. 2014; Reschechtko et al. 2014). The present results suggest that perturbation of a system in the ORT direction, either externally imposed or intentional, can lead to a faster sharing drift, i.e., a faster process within the UCM. While the UCM and ORT subspaces are mathematically orthogonal, this does not mean that the processes they reflect are perfectly

independent of one another. The current results suggest that the two subspaces may be weakly coupled such that a drift in one of them leads to a drift in the other with a comparable time constant. The similar time constants for the force drift and sharing drift observed by Ambike et al. (2015) support this hypothesis.

Anticipatory control of multi-element action

Anticipatory control of an action involves two distinct components. First, there are changes in performance variables in anticipation of the mechanical effects of a planned action, perturbation, or reaction. Examples include anticipatory postural adjustments (APAs, reviewed in Massion 1992) and grip force adjustments seen prior to motion of handheld objects (reviewed in Flanagan et al. 2006). Second, there are feed-forward changes in synergies stabilizing performance variables that the person plans to change quickly; these are addressed as anticipatory synergy adjustments (ASAs, Olafsdottir et al. 2005; Shim et al. 2005). ASAs are seen across tasks, typically earlier than APAs and grip force adjustments, about 200–300 ms prior to the action initiation (Shim et al. 2006; Klous et al. 2011; Krishnan et al. 2011).

Note that the drop in the synergy index during ASA can result from an increase in V_{ORT}, a drop in V_{UCM}, or both (e.g., Arpinar-Avsar et al. 2013). In our experiments, ASAs were primarily induced by an increase in V_{ORT} in the absence of consistent changes in V_{UCM}. In the two-person conditions, the two CNSs were not coupled in any way except the visual feedback on F_{TOT}, so feed-forward ASA observations are very much non-trivial. No F_{TOT} changes occurred during the ASA time interval, meaning that no changes in the visual feedback on F_{TOT} could have been observed by the subjects.

The observation of ASAs in the two-person conditions remains without a convincing explanation. One possibility is that one of the subjects (or both) started to fidget in preparation to the force pulse time, and this potentially could result in larger force deviations from the target. The resulting force deviations, however, were corrected by the other subject and therefore average F_{TOT} was not visibly affected even though this hypothetical "fidgeting" was reflected in the inter-trial variance. This interpretation for ASAs in the two-person condition is different from the earlier interpretation of ASAs as functionally meaningful phenomena reflecting purposeful destabilization of a performance variable in preparation to its quick change (Olafsdottir et al. 2005; Klous et al. 2011). It is possible that ASAs may have different origins, partly supported by the fact that ASAs in the one-person condition started significantly earlier compared to the two-person conditions (350 vs. 175 ms).

Concluding comments

The main purpose of the present study was to investigate the ability of two CNSs to produce force-stabilizing synergies while being linked only by feedback on the performance variable (F_{TOT}). When compared to the performance in one-person conditions, the collaborating CNSs showed a qualitatively similar ability to stabilize F_{TOT}, but with larger indices of synergy due to the larger variance within the UCM. These findings also suggest that, compared to individual action, two CNSs have more difficulty following a single optimization principle. Somewhat surprisingly, we observed anticipatory synergy adjustments in two-person tasks, a phenomenon which so far has only a tentative explanation. Taken together, the results demonstrate that two CNSs are able to organize motor synergies stabilizing a combined output when coupled by visual feedback only and therefore speak in favor of synergic schemes based on sensory feedback loops.

There are certain drawbacks of the current experimental design. In particular, each subject used four fingers (index and middle fingers of both hands) in the one-person condition and only two fingers in the two-person condition. This was done to keep the number of elements involved in the task constant; however, the number of elements controlled by each individual CNS changed between the two conditions. This is a potentially confounding factor, which cannot be easily eliminated. Another drawback is the fact that the subjects performed a virtual task, in the absence of a natural physical coupling with the associated sensory signals. This limits generalization of the conclusions to more ecological tasks, especially keeping in mind that, in everyday actions and clinical applications, cooperative tasks involve both visual and mechanical contact. Such more ecological tasks are in our plans for future research. In particular, we hope to address inter-personal synergies in prehensile tasks involving manipulation of real objects.

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