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Interpersonal Synergies: Static Prehension Tasks Performed by Two Actors

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Abstract

We investigated multi-digit synergies stabilizing components of the resultant force vector during joint performance of a static prehension task by two persons as compared to similar tasks performed by a single person using both hands. Subjects transferred the instrumented handle from the right hand to the left hand (one-person condition) or passed that handle to another person (two-person condition) while keeping the handle's position and orientation stationary. Only three digits were involved per hand, the thumb, the index finger, and the middle finger; the forces and moments produced by the digits were measured by six-component sensors. We estimated the performance stabilizing synergies within the uncontrolled manifold (UCM) framework by quantifying the inter-trial variance structure of digit forces and moments. The analysis was performed at three levels: between hands, between virtual finger and virtual thumb (imagined digits producing the same mechanical variables as the corresponding actual digits combined) produced by the two hands (in both interpersonal and intrapersonal conditions), and between the thumb and virtual finger for one hand only. Additionally, we performed correlation and phase synchronization analyses of resultant tangential forces and internal normal forces. Overall, the one-person conditions were characterized by higher amount of inter-trial variance that did not affect resultant normal force components, higher internal components of normal forces, and stronger synchronization of the normal forces generated by the hands. Our observations suggest that in two-person tasks, when participants try to achieve a common mechanical outcome, the performance stabilizing synergies depend on non-visual information exchange, possibly via the haptic and proprioceptive systems. Therefore, synergies quantified in tasks using visual feedback only may not be generalizable to more natural tasks.

Keywords

interpersonal coordination; synergy; prehension; uncontrolled manifold; internal force

1. Introduction

Two-person interactions are common in everyday activities including passing a hand-held object to another person or holding that object with another person. In such actions, each person must coordinate his or her individual actions with the other to achieve a common mechanical outcome. An individual cannot perfectly predict the changes in mechanical variables that his or her partner will produce, so stable performance of two-person tasks is challenging and must rely on sensory information. Several recent studies have explored variability and stability of two-person actions and reported higher accuracy and higher stability indices in two-person tasks as compared to similar tasks performed by one person (Matsumoto and Inui 2013, 2015; Mojtahedi and Santello 2015; Romero et al. 2015; Solnik et al. 2015). However, these results contrast with several earlier studies (Knoblich and Jordan 2003; Bosga and Meulenbroek 2007) which reported lower accuracy in two-person tasks when compared to those performed by a single person.

In contrast to many common inter-personal interactions, none of the aforementioned studies involved direct haptic contact between subjects as they performed collaborative tasks; instead, the subjects could only use visual information to coordinate their actions. The availability of haptic (and proprioceptive) feedback is likely to play a large role in the way subjects interact with one another and objects they collectively control. Among others, low-latency haptic reflex/feedback mechanisms (cf. “microslips” Tremblay and Curkosky 1993) contribute significantly to the control of held objects (Augurelle et al. 2003; Whitney et al. 2004). The current study utilizes a novel prehension task in which natural haptic and proprioceptive feedback is available to both subjects as they grasp an instrumented handle and pass it to one another. It is a comprehensive exploration of multi-digit synergies stabilizing the combined action of the sets of digits, i.e., prehension synergies (reviewed in Zatsiorsky and Latash 2008), in one-person and two-person actions.

Two of the previous studies mentioned (Romero et al. 2015; Solnik et al. 2015) used the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999) to quantify the structure of inter-trial variance at the level of elements involved in the tasks (joint rotations and finger forces, respectively). Within the UCM hypothesis, inter-trial variance of the elemental variables is quantified in two sub-spaces: variance in the UCM sub-space (V_{UCM}) does not affect the selected performance variable, while variance in the sub-space 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 in Latash et al. 2002, 2007). Prehension synergies are involved in natural hand manipulation tasks based on redundant (Bernstein 1967; more precisely, *abundant*, Latash 2012) sets of digits. This abundance of elements offers the central nervous system (CNS) an opportunity to organize them into task-specific synergies stabilizing salient performance variables (Schöner 1995; Latash 2008). In static prehension tasks, such variables include resultant forces/moments acting on the hand-held object as well as internal forces (e.g., the grip force).

Traditionally, single-hand actions have been described as based on a two-level hierarchy (Arbib et al. 1985). At the upper level, the task is shared between the thumb and a virtual

finger (VF, an imagined digit with the same mechanical action as the involved fingers combined). At the lower level, VF action is shared among the actual fingers. If a prehensile task is performed by two hands (either both hands of the same person, or two hands that belong to two different persons), another level may be assumed corresponding to sharing the task between the hands. Until recently, most studies of prehension synergies within the described framework involved actions performed by one person. In particular, those studies discovered a trade-off between levels of hierarchical control involved in multi-digit actions (Gorniak et al., 2007, 2009a,b).

Based on the mentioned studies (Romero et al. 2015; Solnik et al. 2015), we hypothesized that two-person prehensile tasks will show higher synergy indices stabilizing the main force components as compared to similar tasks performed by a single person using both hands (Hypothesis 1). The trade-off between synergies at different hierarchical levels (Gorniak et al. 2007, 2009a) suggests that at a within-hand level, synergies will show larger indices in one-person conditions (Hypothesis 2). We explored both hypotheses with respect to the three main force/moment vectors acting on the grasped object in the plane of grasping defined as the plane passing through the centers of the nominal digits force application (centers of the corresponding force sensors): normal force, tangential load-resisting force, and moment of force. Our findings have disproved both hypotheses. We found that both the inter-hand and intra-hand synergies are stronger in single-person tasks. The finding suggests a major role of non-visual, such as haptic and proprioceptive, information in two-person prehension tasks.

2. Methods

Subjects

Twelve subjects (5 female) between 23 and 33 years of age participated in this study. For the two-person tasks, subjects were randomly matched to one another in order to form twelve subject pairs. To control for the effect of handedness, we enrolled only self-reported right-handed subjects who used their right hand for eating and writing. Focusing on the right-handers only (and involving the right hands in the two-person conditions, see later) was a practical decision with the purpose to limit the duration of the experiment. Each subject performed in both one-person and two-person conditions. In the two-person condition, each subject participated twice: one subject held the top part of the handle while the other subject held the bottom part (see below), and then the subjects switched. Across all conditions, the right hand always held the top part of the handle, while the left held the bottom part.

None of the subjects had a history of serious hand injuries or any neurological conditions that would interfere with the prehension task. Subjects' dominant hands, from the distal wrist crease to tip of the longest finger, were 18.2 ± 0.7 cm long, and $8.9 \text{ cm} \pm 0.6$ cm wide at the metacarpal level. Each subject provided informed consent according to procedures approved by the Pennsylvania State University Office of Research Protection. Due to technical problems during the experiment (damaged force sensor), data from only eleven subjects and, therefore, eleven pairs were available for analysis.

Apparatus

For the experimental procedure, subjects manipulated an instrumented handle. This handle was 140 mm × 21 mm × 34 mm and instrumented with six multi-axis force/torque transducers (Nano 17, ATI Industrial Automation, Apex, NC) operating as a networked force/torque system (Net F/T, ATI Industrial Automation). The force sensors measured forces and moments generated at the fingertips (Figure 1A). Four sensors were mounted on the *finger side* of the handle. Finger-side sensors were mounted at 15 mm and 45 mm from the center of the side (so their centers were all 30 mm from one another). Two sensors were mounted on the opposing *thumb side* of the handle. The centers of thumb side sensors were 30 mm from the center such that each sensor was between a pair of sensors on the finger side of the handle. The *grip width* – defined as the distance between the parallel planes defined by the outside faces of the thumb and finger sensors – was 60 mm. The surface of each sensor was covered with a 320-grit sandpaper where it contacted the fingertip to increase friction between digits and the sensors. A circular bubble level was attached to the top of the handle (height = 17 mm, radius = 15 mm, resolution $\pm 1^\circ$) to provide subjects with consistent feedback on handle orientation. An additional metal weight was fixed at the bottom of the handle, bringing the total weight of the instrumented manipulandum (including force sensors and circular level) to $W = 6.3$ N.

The origin of the handle coordinate frame was fixed at the geometrical center of the handle. The vertical X-axis was positive in upward direction, while horizontal Z-axis was positive in the direction of thumb sensors. Force data from the force/torque sensors were digitized at 100 s^{-1} and streamed via Ethernet to a desktop computer using ATI Net Box integrated amplifier/servers. A custom computer program running in a LabVIEW environment (National Instruments, Austin, TX) saved these data for subsequent offline analysis.

Experimental procedure

The order of presenting the conditions to subjects was randomized. During the one-person condition, the subject sat on a chair and held the handle vertically using both hands, with arms abducted at 45° , elbows flexed at 90° , and 0° wrist flexion, with thumb sensors facing him or her (Figure 1B). Digits of the right hand – right index (I_R), right middle (M_R), and right thumb (T_R) – were placed on the top three force sensors, while left index (I_L), left middle (M_L), and left thumb (T_L) were placed on the three bottom sensors. During this task, subjects transferred the handle from the right hand to the left hand and back again cyclically for 2 min. Each subject grasped and released the handle using finger flexion and extension only, without any arm movement, while attempting to keep handle orientation and position as steady as possible. As a result, the task consisted of the following steady-state phases following each other in this particular order: holding the handle with both hands, holding it with only the right hand, holding it with both hands, holding it with only the left hand, holding it with both hands, etc. Each phase lasted for about 4 s in order to reach a quasi-static state for further analysis. To avoid the effect of external audio cues, subjects counted the timing of each phase silently. In the one-person condition, only an investigator and the subject performing the task were present in the room. The other subject, previously assigned to the pair, waited in a separate room.

In the two-person condition, two subjects sat on chairs next to one another (Figure 1C). The subject to the right of the handle, held the handle with his or her right hand (I_R , M_R , and T_R) placed on the top three sensors, while the subject on the left held the handle with his or her left hand (I_L , M_L , and T_L) placed on the bottom three sensors. For the arm involved in the task, each subject's forearm-hand configuration was similar to that during the single-person condition. The subjects performed a cyclic transfer of the handle from one person to the other for 2 min, resulting in the following phases: both subjects holding the handle, first subject holding with right hand only, both subjects holding, the second subject holding with left hand only, both subject holding the handle, etc. As in the one-person condition, subjects counted the timing of each grasp phase silently. Subjects could only synchronize grip phases by means of visual and tactile feedback because verbal communication was disallowed. As in the one-person task, subjects in the two-person task were asked to keep the handle position and orientation as steady as possible. In the current paper, we present analysis of the data from the phase of holding the handle with both hands, in both one-person and two-person conditions.

Before the data collection, subjects were given about 1 min of practice trials for each experimental condition. Each trial was repeated twice, and 2-min rest periods were provided between trials. In total, the experimental session lasted about 30 min.

Data analysis

All data analysis was performed off-line using a custom Python code (Python 3.0, Python Software Foundation) and run within the interactive IPython integrated development environment (Pérez and Granger 2007). Prior to data analysis, all digitized signals were low-pass filtered at 10 Hz with fourth-order, zero-lag Butterworth filter. All forces and moments of force were expressed in the handle coordinate frame. In the following text, the force components along Z-axis and X-axis are called normal and tangential forces, respectively. We performed analyses in the grasp plane – the plane passing through the centers of all six force sensors – only.

For both one-person and two-person conditions, individual hand grip phases were identified using thumb forces of the corresponding hand. The first time point when the thumb force exceeded 1 N and was over 1 N for the next 2 s was taken as indicating grip initiation, while the first time point when the thumb force dropped below 1 N was taken as indicating grip release. Two-hand grip phases were defined as the overlaps of the individual hand grip phases. On average, there were 19 two-hand grip phases in the one-person condition, and 18 two-hand grip phases in the two-person condition, identified for each 2-minute trial.

Uncontrolled manifold (UCM)-based analysis—The UCM hypothesis (Scholz and Schöner 1999) assumes that the central nervous system (CNS) organizes redundant elemental variables (digit forces, hand forces, or subject forces at different levels of analysis of this study) to stabilize salient, task-specific variables. This is reflected in the structure of across-trials variance between two subspaces. One subspace (UCM) corresponds to variance among elemental variables that do not change the selected performance variable, V_{UCM} . In contrast, variance among the elemental variables in the subspace orthogonal to the UCM

(V_{ORT}) affects that performance variable. $V_{UCM} > V_{ORT}$ is interpreted as a reflection of a synergy stabilizing the performance variable. Finger force synergies were analyzed with respect to performance variables at three levels of analysis: 1) between-hands analysis (H1–H2 level); 2) between virtual finger (VF) and virtual thumb (VT) analysis (VF-VT level); and 3) within the right (top) hand analysis (within-hand level).

Analysis at the between-hands (H1–H2) level: Successful task performance required that subjects kept the handle in static equilibrium. As such, the following constraints on the resultant tangential force (F_{RES}^T), resultant normal force (F_{RES}^N) and resultant moment of force about Y-axis (M_{RES}^Y) had to be satisfied:

$$F_{RES}^T = F_{RES,R}^T + F_{RES,L}^T = -w \quad (1)$$

$$F_{RES}^N = F_{RES,R}^N + F_{RES,L}^N = 0 \quad (2)$$

$$M_{RES}^Y = M_{RES,R}^Y + M_{RES,L}^Y = 0 \quad (3)$$

where subscripts R and L refer to the right and left hands, while T and N superscripts indicate tangential and normal components.

For the H1–H2 analysis, the performance variables (elemental variables) were F_{RES}^T ($F_{RES,R}^T$ and $F_{RES,L}^T$), F_{RES}^N ($F_{RES,R}^N$ and $F_{RES,L}^N$), and M_{RES}^Y ($M_{RES,R}^Y$ and $M_{RES,L}^Y$). Note that small handle deviations were inevitable; so Equations (1–3), as well as further equations of statics, were satisfied within some error margin.

Analysis at the Virtual Finger–Virtual Thumb (VF-VT) level: The virtual thumb (VT) characterizes an imagined digit with the same mechanical effects as the two thumb (T_L and T_R) forces combined. Similarly, the virtual finger (VF) is defined to have the same mechanical effects as the four fingers (I_R , M_R , I_L , M_L). In the current study, the VF force was computed as the sum of I_R , M_R , I_L , M_L finger forces, while VT force was computed as the sum of T_L and T_R thumb forces.

The static equilibrium equation (Equation 2) can be re-written for the VF-VT level as:

$$F_{RES}^N = F_{RES,VF}^N + F_{RES,VT}^N = 0 \quad (4)$$

which represents the same equilibrium constraint but with the forces arranged differently. In Equation 2, $F_{RES,L}^N$ and $F_{RES,R}^N$ are generated by individual hands (one-person condition) or subjects (two-person condition). In Equation 4, however, both hands contribute to both

$F_{RES,VF}^N$ and $F_{RES,VT}^N$. For the VF-VT analysis, the performance variable (elemental variables) was F_{RES}^N ($F_{RES,VF}^N$ and $F_{RES,VT}^N$).

Analysis at the within-hand level: Previous studies (Gorniak et al. 2007, 2009a,b) revealed the inherent trade-off between force-stabilizing synergies at two hierarchical levels: high indices of synergy at the between-hands level were observed in conjunction with low indices at the within-hand level, and vice-versa. To explore whether performance of the prehension task in the two-person condition displays this trade-off, we quantified the force-stabilizing synergies within the right hand. For within-hand analysis, the performance variables were $F_{RES,R}^T$ and $F_{RES,R}^N$, while elemental variables were the tangential or normal components of the I_R , M_R , and T_R digit forces, respectively.

Analysis of the structure of variance (UCM-based analysis): For all levels of analysis, each elemental variable (digit force or moment) was computed by averaging the relevant force profiles over 0.5-s time intervals around the midpoint of the steady-state part of two-hand grip phases. Next, the UCM analysis was performed in several steps. First, the Jacobian matrix mapping small changes in individual elemental variables onto changes in a performance variable was computed. Then, UCM was computed as the null-space of the Jacobian matrix and the ORT subspace was defined as that orthogonal to the UCM. Next, elemental variables were projected onto UCM and ORT subspaces. Finally, the inter-trial variances of these projections within UCM and ORT subspaces were computed; these variances are addressed in the text as V_{UCM} and V_{ORT} , respectively. An index of synergy (V) stabilizing a performance variable was computed as $V = (V_{UCM} - V_{ORT}) / (V_{TOT})$, where V_{TOT} is total variance. Variances were normalized by the number of degrees of freedom of their corresponding spaces. V was normalized using Fisher's z-transform; this normalized quantity is referred to as V_Z . Positive values of V_Z indicate a force or moment stabilizing synergy (cf. Latash et al. 2001; Scholz et al. 2002).

Analysis of internal forces—In contrast to resultant forces, the internal normal forces were constrained not by an equation but by an inequality: the normal digit forces had to be above the minimum required to prevent slippage given the tangential forces and the friction coefficient k , $F^N > kF^T$. There were no explicit constraints on the internal tangential forces and internal moment. We quantified different components of the internal force by computing the tangential component of internal force (F_{INT}^T , see Equation 5) and the normal component of internal force (grip force, F_{INT}^N , see Equation 6).

$$F_{INT}^T = \sum_i |f_i^X| - \sum_i f_i^X \quad (5)$$

$$F_{INT}^N = \sum_i \frac{|f_i^Z|}{2} \quad (6)$$

where f_i^X and f_i^Z are components of the i^{th} digit force ($i = \text{I}_R, \text{M}_R, \text{T}_R, \text{I}_L, \text{M}_L, \text{T}_L$) in the X and Z directions, respectively.

To explore whether internal forces generated by a hand depended on whether the subject was holding the handle him- or herself versus when someone else was also holding it, we compared each subject's right hand force data when he or she performed the task in the one-person and two-person conditions. For this purpose, we computed the right hand internal tangential and normal forces ($F_{\text{INT},R}^T$ and $F_{\text{INT},R}^N$, respectively):

$$F_{\text{INT},R}^T = \sum_r |f_r^X| - \sum_r f_r^X \quad (7)$$

$$F_{\text{INT},R}^N = \sum_r \frac{|f_r^Z|}{2} \quad (8)$$

where f_r^Z and f_r^X are components of the r^{th} digit force ($r = \text{I}_R, \text{M}_R, \text{T}_R$) in the Z and X directions.

Analysis of within trial co-variation—To maintain the positional and rotational equilibrium of the handle during the transition phase, subjects had to co-vary the finger forces to satisfy the constraints set out in Equations 1–3. For example, the sum of the resultant tangential forces of the right ($F_{\text{RES},R}^T$) and left ($F_{\text{RES},L}^T$) hands had to be equal to the weight of the handle. In contrast, internal forces did not affect the position or orientation of the handle. Therefore, grip forces of the right ($F_{\text{INT},R}^N$) and left ($F_{\text{INT},L}^N$) hands were not directly constrained by the task, only by the requirement of non-slippage. We used cross-correlation and phase synchronization analyses to quantify amount of the within two-hand grip phase co-variation between force pairs – constrained or not constrained – by the task. The whole two-hand grip phase was used including the transition from one-hand to two-hand phase.

The cross-correlation analysis was performed to examine the temporal relation between the grip forces ($F_{\text{INT},R}^N$ vs. $F_{\text{INT},L}^N$) and between the resultant tangential forces ($F_{\text{RES},R}^T$ vs. $F_{\text{RES},L}^T$) of each hand in both one-person and two-person conditions. Force profiles from two-hand grip phase were used in the cross-correlation analysis. We computed the magnitude of cross-correlation between the hand grip forces ($\rho_{F_{\text{INT}}}$) and the resultant hand tangential forces ($\rho_{F_{\text{RES}}}$), as well as the absolute time lag between the hand grip forces ($\tau_{F_{\text{INT}}}$) and the resultant hand tangential forces ($\tau_{F_{\text{RES}}}$). Cross-correlation coefficients were z-transformed before further statistical analysis.

We used phase synchronization analysis to estimate the phase coupling between the grip forces ($F_{\text{INT},R}^N$ vs. $F_{\text{INT},L}^N$) and resultant tangential forces ($F_{\text{RES},R}^T$ vs. $F_{\text{RES},L}^T$) of each hand (one-person condition) or each subject (two-person condition) during the two-hand grip cycles. The phase synchronization between analyzed forces was estimated using relative

phase difference of grip forces (θF_{INT}^N) and relative phase difference of resultant tangential forces (θF_{RES}^T), computed as:

$$\theta F_{RES}^T = \theta F_{RES,R}^T - \theta F_{RES,L}^T \quad (9)$$

$$\theta F_{INT}^N = \theta F_{INT,R}^N - \theta F_{INT,L}^N \quad (10)$$

where $\theta F_{RES,R}^T$, $\theta F_{RES,L}^T$, $\theta F_{INT,R}^N$, and $\theta F_{INT,L}^N$ are instantaneous phases of the corresponding forces, calculated using Hilbert transform (Pikovsky et al 2001). The resultant values – reflecting phase differences – are presented in radians. A phase difference value of zero represents positive co-variation between two signals (in-phase synchronization), while a value equal to π (~3.14 rad) indicates negative co-variation (out-of-phase synchronization). The θF_{INT}^N and θF_{RES}^T values were pooled across cycles and subjects, resulting in two relative phase difference distributions representing one-person and two-person conditions.

Statistical analysis—All descriptive statistics are reported in the text and figures as means and standard errors unless stated otherwise. Non-significant comparisons are indicated in the text as n.s.

One-way repeated-measures ANOVAs were used to test the effects of *Condition* (two levels: one-person and two-person) on F_{INT}^T , F_{INT}^N , $F_{INT,R}^T$, and $F_{INT,R}^N$. A similar ANOVA design was used to test the effect of *Condition* on V at the H1–H2, VF–VT, and within-hand levels of the UCM-based analysis. Repeated-measures ANOVA were used to test the effect of *Condition* (two levels: one-person and two-person) and *Subspace* (two levels: UCM and ORT) on variance of F_{RES}^T , F_{RES}^N , M_{RES}^Y , $F_{RES,R}^T$, and $F_{RES,R}^N$.

Student's t-tests were used to test effects of *Condition* on $\rho_{F_{RES}^T}$, $\tau_{F_{RES}^T}$, $\rho_{F_{INT}^N}$, $\tau_{F_{INT}^N}$. We tested the modality of θF_{INT}^N and θF_{RES}^T distributions in one-person and two-person conditions using the Hartigan's dip test of unimodality (Hartigan and Hartigan 1985). All statistical tests were performed with R (R Core Team 2013, version 3.2.2) software with the significance level set at $p = 0.05$.

3. Results

Task performance

In both one-person and two-person conditions, subjects did not report fatigue or discomfort during the experiment. Further, subjects were able to perform the task without visibly violating static equilibrium of the handle, regardless of the *Condition*. In both conditions, the F_{RES}^T and F_{RES}^N were very close to their equilibrium constraint values. The load-resisting vertical shear force applied to the handle, F_{RES}^T , closely matched the weight of the setup: it was 6.36 ± 0.03 N across the conditions. The magnitude of F_{RES}^N across conditions was close to zero (-0.14 ± 0.04). The magnitude of M_{RES}^Y was also low, on average -56.6 ± 5.4 Nmm for both conditions.

Internal forces

In general, internal tangential forces were relatively small when compared to internal normal forces. The magnitude of normal internal forces was larger when two persons were involved in the prehension task (see Figure 2). For internal components of force, F_{INT}^T was not significantly different between the one-person and two-person conditions (0.15 ± 0.02 N vs. 0.23 ± 0.06 N), while F_{INT}^N was 17.7 ± 1.7 N for the one-person and 22.5 ± 2.3 N for the two-person conditions ($F_{1,10} = 19.68$, $p < 0.001$). We observed a similar pattern of results for the internal force components measured within the right hand, but the effect of *Condition* was not statistically significant: $F_{INT,R}^T$ was 0.06 ± 0.01 N vs. 0.07 ± 0.04 N, and $F_{INT,R}^N$ was 8.86 ± 0.93 N vs. 11.32 ± 1.45 N, for the one-person and two-person conditions respectively.

Analysis of synergies (UCM-based analysis)

We analyzed the structure of inter-trial variance in resultant tangential forces, resultant normal forces, and resultant moments about Y-axis generated by both hands to quantify synergies stabilizing F_{RES}^T , F_{RES}^N , and M_{RES}^Y during the steady-state phase of the task. A graphical representation of the UCM analysis for a representative subject (white circles) and a representative pair of subjects (black circles) is shown in Figure 3. The figure illustrates results of H1–H2 analysis, where performance variables were F_{RES}^T (left panel), F_{RES}^N (middle panel), and M_{RES}^Y (right panel). For F_{RES}^T and F_{RES}^N , variance along lines representing task constraints of performance variables ($F_{RES}^T = 6.3$ N and $F_{RES}^N = 0$ N) is higher for the one-person condition compared to the two-person condition. This was not true for the M_{RES}^Y analysis. Statistical results for this analysis at different levels are presented below.

Analysis at the H1–H2 level—Overall, performance stabilizing synergies between hands or subjects were observed for all performance variables: V_{UCM} values were substantially higher than V_{ORT} in both one-person and two-person conditions. There was a main effect of *Variance* (V_{UCM} vs. V_{ORT}) for F_{RES}^T ($F_{1,10} = 82.72$, $p < 0.001$), F_{RES}^N ($F_{1,10} = 48.52$, $p < 0.001$), and M_{RES}^Y ($F_{1,10} = 21.34$, $p < 0.001$). Figure 4 shows the summary of these results.

On average, the V_{UCM} values were higher in the one-person condition compared to the two-person condition in the analysis of the two force variables. In particular, V_{UCM} for F_{RES}^T was 2.78 ± 0.51 N² vs. 1.86 ± 0.21 N² (n.s., $p = 0.14$) and for F_{RES}^N it was 0.22 ± 0.04 N² vs. 0.06 ± 0.01 N² ($F_{1,10} = 14.16$, $p < 0.001$), for the one-person and two-person conditions, respectively. Conversely, V_{UCM} was somewhat smaller in the one-person condition for M_{RES}^Y , although this effect was not statistically significant (685.3 ± 138.1 N² vs. 824.1 ± 227.2 N²; n.s., $p = 0.45$). V_{ORT} values were very small compared to the V_{UCM} values (F_{RES}^T : $F_{1,10} = 82.72$, $p < 0.001$; F_{RES}^N : $F_{1,10} = 48.52$, $p < 0.001$; and M_{RES}^Y : $F_{1,10} = 21.34$, $p < 0.001$). V_{ORT} values were, on average, higher in the two-person condition for all three performance variables: F_{RES}^T : 0.0012 ± 0.0004 N² vs. 0.0027 ± 0.0007 N² ($p < 0.05$); F_{RES}^N : 0.0029 ± 0.0008 N² vs. 0.0056 ± 0.001 N² ($p < 0.05$); and M_{RES}^Y : 196.32 ± 40.66 (Nmm)² vs. 267.09 ± 44.91 (Nmm)² (n.s.). ANOVA also showed a significant interaction effect *Variance* $\times$ *Condition* for F_{RES}^N ($F_{1,10} = 13.99$, $p < 0.01$), which indicated that

variance values in the one-person condition were larger within the UCM space but smaller within the ORT space.

The index of synergy (V_Z) analysis reflected the results described above (see Figure 5). In particular, V_Z values were higher in the one-person condition than in the two-person condition, when computed with respect to F_{RES}^T (3.9 ± 0.14 vs. 3.4 ± 0.12 ; $F_{1,10} = 11.86$, $p < 0.01$), F_{RES}^N (2.2 ± 0.12 vs. 1.4 ± 0.13 ; $F_{1,10} = 21.44$, $p < 0.001$) and M_{RES}^Y (0.6 ± 0.07 vs. 0.4 ± 0.11 ; n.s., $p = 0.15$).

Analysis at the VF-VT level—We quantified the synergies between resultant normal forces of VF and VT ($F_{RES,VF}^N$ and $F_{RES,VT}^N$) stabilizing the resultant normal force acting on the handle (F_{RES}^N). In general, performance stabilizing synergies at the VF-VT level were present for both one-person and two-person conditions: V_{UCM} was larger than V_{ORT} in both conditions ($F_{1,10} = 39.16$, $p < 0.001$). However, the effect of *Condition* was below the significance level ($p = 0.067$). In the one-person condition, V_{UCM} values were slightly lower than in two-person condition, but no significant effect of *Condition* was seen (11.06 ± 2.29 N² vs. 16.51 ± 2.8 N², respectively, n.s.). Similarly, V_{ORT} values were, on average, smaller in one-person condition than in two-person condition (0.002 ± 0.0008 N² vs. 0.005 ± 0.001 N², respectively, n.s.). The index of synergy values mirrored the aforementioned results:

V_Z values were positive for both one-person and two-person conditions, without a difference between the conditions (4.18 ± 0.13 vs. 4.08 ± 0.13 ; n.s.).

Analysis at within-hand level—We quantified synergies in the spaces of tangential and normal components of the I_R , M_R , and T_R digit forces with respect to $F_{RES,R}^T$ and $F_{RES,R}^N$. The within-hand analysis showed performance stabilizing synergies only with respect to normal resultant forces. For the $F_{RES,R}^N$ -related analysis, V_{UCM} was consistently higher than V_{ORT} ($F_{1,10} = 19.62$, $p < 0.01$), while for the $F_{RES,R}^T$ -related analysis V_{ORT} was higher than V_{UCM} ($F_{1,10} = 13.74$, $p < 0.01$).

There were no significant effects of *Condition* ($p > 0.15$) and no significant *Variance* $\times$ *Condition* interactions for these analyses. On average, in the $F_{RES,R}^N$ -related analysis, V_{UCM} was larger and V_{ORT} was smaller in the two-person condition compared to the one-person condition (V_{UCM} : 12.14 ± 2.51 N² vs. 15.55 ± 4.17 N²; V_{ORT} : 0.05 ± 0.009 N² vs. 0.01 ± 0.002 N² for the one-person and two-person conditions, respectively). In the $F_{RES,R}^T$ -related analysis, both variance indices were, on average, larger in the one-person condition: 0.28 ± 0.06 N² vs. 0.27 ± 0.04 N² for V_{UCM} , 0.71 ± 0.13 N² vs. 0.46 ± 0.04 N² for V_{ORT} for the one-person and two-person conditions, respectively.

Consistent with the presented differences between V_{UCM} and V_{ORT} , V_Z values were positive when computed with respect to $F_{RES,R}^N$ (2.63 ± 0.11 vs. 3.23 ± 0.16 , for the one-person and two-person conditions, respectively; $F_{1,10} = 11.73$, $p < 0.01$). In contrast, V_Z values were negative for $F_{RES,R}^T$ (-0.56 ± 0.22 vs. -0.36 ± 0.15 , for the one-person and two-person conditions, respectively, n.s., $p = 0.31$).

Within trial co-variation analysis

We explored the amount of within trial co-variation between hands (one-person) or subjects (two-person) for force pairs constrained by the task (resultant tangential forces; $F_{RES,R}^T$ vs. $F_{RES,L}^T$) and forces that only had to satisfy an inequality imposed by the friction conditions (see Methods, internal normal forces; $F_{INT,R}^N$ vs. $F_{INT,L}^N$). Typical force traces used in this analysis for the two-person condition are shown in Figure 6. Note the synchronous changes of $F_{RES,R}^T$ and $F_{RES,L}^T$, while the other pair of forces, $F_{INT,R}^N$ vs. $F_{INT,L}^N$, fails to show synchronous changes.

Cross-correlation analysis—The maximum cross-correlation coefficient ($\rho_{F_{RES}^T}$) between $F_{RES,R}^T$ vs. $F_{RES,L}^T$ was -0.99 ± 0.07 for the one-person and -0.99 ± 0.06 for the two-person condition ($t = 3.06$, $p < 0.01$). The absolute lag between $F_{RES,R}^T$ vs. $F_{RES,L}^T$ ($\tau_{F_{RES}^T}$) was close to zero: 2.2 ± 0.02 ms and 2.2 ± 0.01 ms for the one-person and two-person conditions, respectively, without a difference between the two conditions. The maximum cross-correlation coefficient ($\rho_{F_{INT}^N}$) between $F_{INT,R}^N$ vs. $F_{INT,L}^N$ was -0.80 ± 0.12 and -0.48 ± 0.12 for the one-person and two-person conditions, respectively ($t = 3.16$, $p < 0.01$). The absolute lag between $F_{INT,R}^N$ and $F_{INT,L}^N$ ($\tau_{F_{INT}^N}$) was 19.3 ± 8.2 ms vs. 81.5 ± 22.4 ms for the one-person and two-person conditions, respectively ($t = 2.61$, $p < 0.05$).

Phase synchronization analysis—There was a striking disparity between phase differences of $F_{RES,R}^T$ vs. $F_{RES,L}^T$ and $F_{INT,R}^N$ vs. $F_{INT,L}^N$ (see Figure 7). The effect of equilibrium constraint was clearly seen for phase synchronization between $F_{RES,R}^T$ and $F_{RES,L}^T$ ($\theta_{F_{RES}^T}$). The distributions of the $\theta_{F_{RES}^T}$ for both conditions were very similar – with most frequent values close to 3.14 rad, suggesting a strong negative co-variation (3.18 rad and 3.14 rad for the one-person and two-person conditions, respectively). In contrast, the distributions of the relative phase difference between $F_{INT,R}^N$ and $F_{INT,L}^N$ ($\theta_{F_{INT}^N}$) were different between the two conditions. The distribution of $\theta_{F_{INT}^N}$ in the one-person condition had a narrow shape with one clear peak (at 2.78 rad), while in the two-person condition, the $\theta_{F_{INT}^N}$ distribution was wider and had two peaks (at 1.29 rad and 4.03 rad). The Hartigans' dip test of unimodality confirmed that only the distribution of $\theta_{F_{INT}^N}$ in the two-person condition was not unimodal, and at least bimodal ($D = 0.009$, $p < 0.001$).

4. Discussion

Our observations falsified both main hypotheses, suggesting that prehension synergies during two-person actions are strongly dependent on non-visual, haptic and/or proprioceptive, information. Indeed, the first hypothesis based on earlier studies using visual coupling between the two actors (Matsumoto and Inui 2013; Mojtahedi and Santello 2015; Romero et al. 2015; Solnik et al. 2015) was that the between-hand synergies would be stronger for two-person actions compared to the same tasks performed by a single person. In fact, the synergy indices were significantly higher for the one-person condition for the resultant F^N , while the differences for the F^T and moment were in the same direction (higher in the one-person condition) but not significant. This was associated with both larger amount of variance that did not affect force/moment vector components (V_{UCM}) and lower amount of variance that did (V_{ORT}). Our second hypothesis followed the first one under the

assumption of a trade-off between levels of control within a hierarchy (Gorniak et al. 2007, 2009a,b). In fact, as opposed to the predicted effects, we observed stronger synergies controlling the normal force in one-person conditions compared to two-person conditions. No synergies stabilizing other force/moment components were seen.

We also performed exploratory analysis of within-a-trial synchronization of forces produced by the two hands in both inter- and intrapersonal tasks. These analyses revealed a striking difference between one-person and two-person conditions with respect to the control of the grip force (internal normal force). The results once again pointed at an advantage of tasks performed by a single person: individuals displayed strong synchronization of forces produced by their hands. No such synchronization was seen in similar tasks performed by two persons. These results underscore the potential shortcoming of experiments performed in virtual reality – with only visual feedback coupling the two actors – to neglect the contributions of the haptic and proprioceptive information exchange that is present in ecological tasks.

4.1. Synergic control of action in two-person tasks

Studies involving inter-personal motor coordination form two groups that differ by the nature of the tasks. Studies within the first group required participants to perform individual tasks, not a common task, while being linked by visual (Schmidt et al. 1990; Fine and Amazeen, 2011; Fine et al. 2013), auditory (Shockley et al. 2003; Stoffregen et al. 2009), or haptic information (van der Wel et al. 2011). Some of the studies addressed spontaneous movements, such as postural sway (e.g., Shockley et al. 2003; Stoffregen et al. 2009), while other studies explored intentional movements such as moving hand-held pendulums or moving into targets (e.g., Schmidt et al. 1990; Fine and Amazeen, 2011; Fine et al. 2013). Several such studies have reported patterns of behavior similar to those expected from a single person coordinating multiple limbs (Schmidt et al. 1990; Fine and Amazeen 2011; Fine et al. 2013). In particular, both one-person and two-person tasks show stabilization of the relative phase during rhythmic movement of two limbs (Black et al. 2007; Riley et al. 2011).

Studies within the second group linked participants by a common mechanical outcome, like lifting a virtual object (Knoblich and Jordan 2003; Bosga and Meulenbroek 2007) or the production of a rhythmical (Matsumoto and Inui 2013) or non-rhythmical (Solnik et al. 2015) pattern of total finger force. All these studies explored intentional movements defined by an explicit task. The current study is similar to those experiments in that our subjects were supposed to keep certain resultant mechanical variables acting on the handle at levels compatible with the equations of statics; however, natural somatosensory (haptic and proprioceptive) coupling was available to assist the two actors.

We explored *prehension synergies*, defined as co-varied patterns of involvement of elemental variables (those produced by individual effectors such as hands or digits) that preserve a magnitude of a performance variable to which they all contribute (Zatsiorsky and Latash 2004, 2008). This is not the only meaning of the term *synergy* in motor control (Latash 2008). In the clinical literature, 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 the motor control literature, synergy has most often been used to denote groups of variables, which show parallel scaling over the time course of an action or with changes in parameters of a motor task (d'Avela et al. 2003; Ivanenko et al. 2004; Ting and Mcpherson 2005). Using synergies has been viewed as a means of alleviating the problem of motor redundancy (Bernstein 1967) by reducing the number of variables manipulated by the CNS.

The definition of synergy utilized in the present study is related to the *stability of action*. Such stability is a crucial feature of natural movements, which are characterized by variable and unpredictable changes in both the environment and intrinsic states of the body. Analysis of inter-trial variance components, V_{UCM} and V_{ORT} , has been used to quantify the stability of multi-digit actions. This analysis is based on the idea that consecutive trials always start from varying initial states. As a result, trajectories seen across individual trials are expected to diverge in unstable directions and converge in stable directions. If one computes across-trials variance at a particular phase of the action, larger values are expected in directions of lower stability while lower values are expected in directions of high stability. So, if a performance variable is selectively stabilized, higher variance is expected within its UCM compared to variance orthogonal to the UCM leading to the synergy signature: $V_{UCM} > V_{ORT}$.

Two earlier studies (Romero et al. 2015; Solnik et al. 2015) reported higher proportion of V_{UCM} in the total variance corresponding to stronger synergies in two-person actions. One of them (Solnik et al. 2015) used a multi-finger accurate force production task and reported much higher V_{UCM} values in two-person tasks compared to similar tasks performed by one person. Our current findings are strikingly different: Two-person conditions showed significantly lower V_{UCM} compared to one-person conditions for F^N (see Figure 4). Both tasks required the production of accurate force magnitudes. A major difference was in the task-related feedback, visual in the earlier study and natural (visual, haptic, and proprioceptive) in the current study. This difference suggests that characteristics of synergies discovered in virtual reality may not be generalizable to synergies in more natural tasks.

4.2. Prehension synergies in a hierarchical system

Several earlier studies documented trade-offs between synergies at different levels of a hierarchical system involved in the control of prehensile actions (Gorniak et al. 2007, 2009a; Sun et al. 2011; Wu et al. 2012). These findings could be related to the method of computation of the synergy index. For example, for one-hand prehensile tasks, at the higher level of the hierarchy (the virtual finger-thumb, VF-TH level), large amounts of V_{UCM} increase the synergy index. On the other hand, large V_{UCM} implies high variance of both thumb and VF forces. At the lower level of the hierarchy, co-variation of finger forces is analyzed with respect to the VF force. At that level, the VF force variance is, by definition, V_{ORT} , and its large amounts bring the synergy index down. It is possible to have strong synergies at both levels as shown in experiments for synergies stabilizing tangential force during one-hand prehensile tasks (Gorniak et al. 2009; Sun et al. 2011). Nevertheless, the overall tendency for synergy indices computed at the two levels is to compete with each other (e.g., Wu et al. 2012; Singh et al. 2014).

Our results corroborate the idea of a trade-off between synergies at the highest level of the assumed hierarchy (the task shared between the two hands; cf. Matsumoto and Inui 2015) and the lower level (within-a-hand level). Indeed, while there were strong synergies stabilizing all the main mechanical variables F^N_{RES} , F^Y_{RES} , and M^Y_{RES} , at the upper level, no such synergies were seen at the within-a-hand level for F^T . There were strong synergies stabilizing F^N at both levels, but the differences between the two conditions were opposite: the synergy index was higher for the one-person condition at the upper level, and it was higher for the two-person condition at the lower (within-a-hand) level (Figure 5). Hence, our results are compatible with the general idea that there is a trade-off between synergies at different levels within a hierarchical system.

While the focus of our study and some of our results are similar to those by Matsumoto and Inui (2015), there are significant differences between the tasks. We used a prehension task with a free-moving handle in contrast to the isometric pressing used by Masumoto and Inui; hence, our task required satisfying equations of statics with respect to six resultant force/moment variables. Another important difference is that the Masumoto and Inui study explicitly imposed periodicity by altering the target force level for both subjects in synchrony. In contrast, our subjects performed the task in a self-paced fashion; guidance on the action timing was only loosely provided by the instruction. Despite these differences, there is consistency in the findings of higher performance synchrony for a single-person than two-person task. With regard to “force complement” (Masumoto and Inui 2015) – which is a measure related to our UCM variance – individuals in the one-person condition displayed more complementary force production. This could be related to better knowledge of one’s own force production as compared to knowledge of the partner’s force; hence, subjects adopted a more stereotypical strategy, potentially to aid the partner by making one’s own actions more predictable – a strategy that has been noted by Sacheli and colleagues (2013).

4.3. Role of sensory information in synergic control

Several theoretical schemes have been offered for synergic control including those based on optimal feedback control (Todorov and Jordan 2002), intrinsic CNS loops (Latash et al. 2005), feed-forward schemes (Goodman and Latash 2006), and sensory feedback loops (Martin et al. 2009). Our results suggest that sensory loops are indeed important, at least for prehension synergies. Moreover, they suggest that different sensory modalities may preferentially affect such synergies. When the subjects were coupled by visual information only (Solnik et al. 2015), they showed much higher synergy indices in the two-person condition. In contrast, when natural haptic and proprioceptive coupling was allowed in addition to visual feedback, higher synergy indices were observed under the one-person conditions.

These observations have potentially important implications for both basic and clinical research. First, many motor control studies have been performed under “virtual reality” conditions, when the subjects received information on their actions mediated by visual feedback. These studies included manipulations of visual information so that it could be distorted and differ from the actual actions performed by the subjects. Examples include experiments with visual rotation (Imamizu and Kawato 2008; Krakauer and Mazzoni 2011)

as well as more subtle modifications of visual feedback that were not perceived by the subjects as distorted (Wu et al. 2014). Our results suggest that the synergic control of actions could be different under such conditions as compared to natural feedback conditions. Note that a recent study of two-person hopping tasks has provided evidence for the importance of somatosensory information exchange for inter-personal synergies that were absent during visual contact only (Slomka et al. 2015).

Second, the results also have direct implications on the use of virtual reality in rehabilitation. Recent progress in, and broad use of virtual reality (reviewed in Weiss et al. 2014) is based on an assumption that the patterns and neural control of actions in such environments are similar to those observed in actual behavior. Our results suggest that this may not be true: two-person tasks in a virtual reality environment (only visual feedback linked kinetic variables) led to a dramatically different structure of variance, reflecting different stability of performance as compared to natural tasks. This shortcoming may be mitigated by the use of simulated haptic information (Danieau et al. 2013; Giggins et al. 2013), but using such information for multi-element synergies has not been explored.

4.4. Within-a-trial analysis as a window into synergies

Since the inauguration of the UCM hypothesis (Scholz and Schöner 1999), quantitative exploration of synergies within the UCM-based method has been based on analysis of variance over multiple trials (reviewed in Latash 2008). Developing a method to characterize synergies based on individual trials would be of particular importance for clinical studies where the patients may not be able to perform the multiple trials necessary for the inter-trial variance analysis.

To our knowledge, only one attempt was made to develop a “single-trial UCM analysis” (Scholz et al. 2003), and this extension of the method was valid only under specific, heavily constrained conditions. Another method of analysis of synergies based on individual trials has been suggested recently based on measurement of deviations of a multi-element system along the UCM and ORT spaces (Scholz et al. 2011; Mattos et al. 2011, 2015). This method compares motor equivalent (ME, within the UCM) and non-motor equivalent (nME, within ORT) deviations of the system during quick actions. If stability along ORT is higher, larger ME deviations are expected compared to nME deviations. This method offers another set of indices as a proxy of stability. So far, no quantitative comparison of the V_{UCM} vs. V_{ORT} and ME vs. nME indices has been performed.

Analysis of co-variation of elemental variables over time is confounded by the existence of two main factors: Synergic control and corrections of the ongoing action. Consider, for example, accurate force production by two effectors, e.g., fingers pressing on individual force sensors. A synergy stabilizing total force is expected to lead to negative co-variation of the individual finger forces. On the other hand, if a subject perceives deviation of the actual total force from the desired level (via visual or somatosensory feedback), a correction may be introduced leading to a change in both finger forces in the same direction, i.e. leading to their positive co-variation. If high-resolution feedback is available, the latter factor may be expected to dominate. If the subject does not correct performance due to poor feedback resolution and/or low motivation, the former factor may be expected to lead to negative

finger force co-variation. Several studies documented both effects (Ranganathan and Newell 2008a,b; Hu and Newell 2011a) and explored them theoretically (Hu and Newell 2011b).

In the current study, both hands – regardless of whether they belonged to the same person or to two different person – made mechanical contact with the handle, which provided direct feedback on changes in the tangential forces but not necessarily in the normal forces. This was reflected, in particular, in the close to zero time delays in the cross-correlation functions in the F^T -related analysis and by the close to 3.14 rad values of θF^T_{RES} in the phase synchronization analysis for both conditions. Indeed, a change in F^T produced by one hand immediately changed the gravitational load experienced by the other hand resulting in its F^T changes due to the elastic properties of the peripheral tissues. These effects were common between the one-person and two-persons conditions suggesting that they were indeed of a purely mechanical origin.

Analysis of the normal forces showed similar results in the one-person condition only. In this condition, we observed a short time delay of the peak of the cross-correlation function and a unimodal distribution of θF^N_{INT} with one clear peak at about 2.8 rad. These results suggest a feed-forward process that defined the correlated changes in the normal forces when one person used both hands. In the two-person condition, however, the peak of the cross-correlation function was relatively low and it occurred at the time delay of about 80 ms, compatible with the action of so-called long-loop reflexes (or pre-programmed reactions) (Johansson and Westling 1984; Häger-Ross et al. 1996; Johansson 1998). The bimodal distribution of θF^N_{INT} also suggested the action of feedback loops, possibly reflecting a “leader-follower” pattern (Reed and Peshkin 2008; Sacheli et al. 2013; Ganesh et al. 2014; Mojtahedi and Santello 2015).

Studies of phase synchronization have been used in the field of motor control for many years (Walsh 1997; Serrien and Swinnen 1998; Rearick et al. 2002, 2003; Roerdink et al. 2013). We hope that the current study would ultimately lead to a method sensitive to synergic adjustments of elemental variables and also able to distinguish between feed-forward and feedback mechanisms that contribute to such adjustments.

4.5. Concluding comments

We would like to acknowledge a few shortcomings of this study. First, we report results of analysis of synergies only with respect to some performance variables and only at some of the levels of analysis. Indeed, synergies could be quantified with respect to the other component of the shear force (orthogonal to the grasp plane) and with respect to other moment components (as in Shim et al. 2005). Also, we describe the data at three levels of analysis, between hands, between the virtual finger and virtual thumb, and between the digits of the right hand.

Our study involved right-handed subjects only. Moreover, in the two-person conditions, only the two right hands were tested. This is a shortcoming given the documented differences in the control of the dominant and non-dominant extremities (e.g., Sainburg 2005). Testing the left hands of the right-handed subjects would definitely strengthen the conclusions.

However, this would prolong the testing session considerably and could lead to fatigue. Exploring such synergies in left-handers would be a whole new study.

The analysis of cross-correlation functions and phase synchronization was done for only one resultant force component and one internal force component. Since this was an exploratory goal, we have decided not to perform similar analyses for other force/moment components, both resultant and internal. Adding more analyses would make the paper too heavy. Hence, we decided to limit our presentation to a subset of analyses most relevant to the specific hypotheses.

Another potentially interesting issue is addressing interactions among synergies within a multi-level hierarchy. Our task involves three levels at the mechanical level of analysis: sharing the task between the two hands (controlled by a single CNS or by two CNSs), sharing each hand's contribution between the thumb and VF, and then sharing the VF output between the actual fingers. While our results confirm the trade-off between synergies at the top level and at the thumb-VF level, the role of other levels remains unclear. This is a topic for a future study.

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Figure 1.

The instrumented handle with six force/torque transducers (panel A). Four sensors were mounted on the finger side of the handle and two sensors were mounted on the opposing (thumb) side of the handle. A circular bubble level was attached to the top of the handle to provide subjects with feedback on handle orientation. The total weight of the instrumented handle was $W = 6.3$ N. On the right, top views show a typical configuration of hands and fingers during the one-person (panel B) and two-person (panel C) conditions.

Figure 2.

Results of the internal force analysis. Averaged across subjects values with standard error bars are shown for the one-person (black) and two-person (grey) conditions. Tangential (F_{INT}^T) and normal (F_{INT}^N) components of internal forces computed for both hands (top panels) and for the right hand only (bottom panels). Note the different scales of the Y-axes in the panels chosen to optimize visual perception of the results.

Figure 3.

An illustration of the UCM-based analysis for a representative subject (white circles) and pair of subjects (black circles). The figure shows individual trial data points for the between-hands analysis, where the performance variables were resultant tangential force (F_{RES}^T , left panel), resultant normal force (F_{RES}^N , middle panel) and resultant moment of force about Y-axis (M_{RES}^Y , right panel). X- and Y-axes correspond to the elemental variables for the right (subscript R) and left (subscript L) hands, respectively. For F_{RES}^T and F_{RES}^N , variance along the UCM direction (line with negative slope) was typically higher for the one-person condition compared to the two-person condition.

Figure 4.

Results of the UCM-based analysis of variance. Averaged across subjects values with standard error bars are shown for the one-person (black) and two-person (grey) conditions. Inter-trial variance along the UCM (V_{UCM} , top row), and variance orthogonal to the UCM (V_{ORT} , bottom row) were computed with respect to the resultant tangential force (F_{RES}^T , left), resultant normal force (F_{RES}^N , middle), and resultant moment of force about Y-axis (M_{RES}^Y , right). Note the different scales of the Y-axes in the panels chosen to optimize visual perception of the results.

Figure 5.

The index of synergy (ΔV_Z) averaged across subjects with standard error bars for the one-person (black) and two-person (grey) conditions. Top row: ΔV_Z with respect to the resultant tangential force (F_{RES}^T) and resultant normal force (F_{RES}^N) for the between-hands analysis. Middle row: ΔV_Z computed with respect to the resultant tangential force ($F_{RES,R}^T$) and resultant normal force ($F_{RES,R}^N$) of the right hand. Bottom row: ΔV_Z for the resultant moment of force about Y-axis (M_{RES}^Y), for the between-hands analysis. Note the different scales of the Y-axes in the panels chosen to optimize visual perception of the results.

Figure 6.

Typical traces of the resultant tangential (F_{RES}^T , left) and internal normal (F_{INT}^N , right) forces during a two-hand grip phase in the two-person condition. Dashed lines represent left hand forces (subscript L), while solid lines represent right hand forces (subscript R).

Figure 7.

Kernel density estimation plots show the distributions of the phase differences pooled across multiple episodes of two-hand grasping phases and subjects for the one-person (dashed line) and two-person (solid line) conditions. Top panel: The distribution of phase differences between the left and right hand internal normal forces (θF_{INT}^N). Bottom panel: The distribution of phase differences between the left and right hand resultant tangential forces (θF_{RES}^T). The black arrows show phase difference values at the distribution modes. A phase difference value of zero indicates positive co-variation between two signals (in-phase

synchronization), while a value close to π (~ 3.14 rad) indicates negative co-variation (out-of-phase synchronization). Note that the distribution of θF_{INT}^N in the two-person condition was at least bimodal.