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Effects of Task Complexity on Coordination of Inter-Limb and Within-Limb Forces in Static Bimanual Manipulation

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Coordination of the hand grip (G; acting normally to the grasping surface) and load forces (L; acting in parallel) in bimanual static tasks was studied. L symmetry (either the magnitude or direction) and frequency were manipulated in healthy participants (N = 14). More complex tasks (i.e., the higher frequency and/or asymmetric ones) revealed expected deterioration in both the task performance (accuracy of the prescribed L force profiles) and force coordination (G/L ratio and G-L correlation) suggesting importance of L frequency and symmetry in prehension activities. However, the same tasks revealed a more prominent deterioration of interlimb than the within-limb force coordination. This could be interpreted by two partly different and noncompeting neural control mechanisms where the coordination of interlimb forces may be based on ad-hoc and task-specific muscle coordination (often referred to as muscle synergies) while the within-limb coordination of G and L could be based on more stable and partly reflex mechanisms.

Keywords: grip, load, coupling, performance, control, hand

Grasping and manipulating objects are the most frequent motor activity of daily life. According to a simple kinetic model, it requires the exertion of a sufficient grip force (G; acting normally to the object's contact surface) to stabilize the object against the load force (L; acting in parallel) that performs the manipulative action. In general, G is adjusted to the physical properties of the object (such as the mass or the surface friction) to prevent slippage that could be caused by the action of L (Flanagan & Wing, 1995; Johansson & Westling, 1988). Although a brief period of G adaptation is needed at the initial phase of interaction with a novel object (Johansson & Westling, 1984), the CNS maintains a close coordination of G and L over a variety of ongoing manipulative actions (Cole & Abbs, 1988; Flanagan & Wing, 1995; Johansson & Westling, 1984) virtually without any time delay between them (Flanagan & Wing, 1995; Jaric, Collins, Marwaha, & Russell, 2006; Zatsiorsky, Gao, & Latash, 2005). As a consequence, G and L control pattern maintains both a relatively low and stable G/L ratio (Johansson & Westling, 1984).

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The most often studied aspects of force coordination in manipulative tasks have been G scaling and G-L coupling. G scaling has been usually assessed through the G/L ratio presuming that in a well-controlled manipulation G should be sufficient to prevent slippage, but not excessive to crush the object or cause a rapid fatigue (Flanagan & Wing, 1995; Johansson & Westling, 1984). G-L coupling has been assessed through the maximum correlation coefficients and the corresponding time lags observed from the cross-correlations function calculated from the force-time series (Flanagan, Tresilian, & Wing, 1993; Flanagan & Wing, 1995; Jaric et al., 2006; Jaric, Knight, Collins, & Marwaha, 2005). However, since most of the studies have observed negligible time lags, simple correlation between G and L has been frequently calculated instead (Flanagan & Wing, 1995; Jaric, Knight et al., 2005; Nowak & Hermsdorfer, 2002). We recently demonstrated that the task performance variables calculated from the differences between the prescribed and the exerted L pattern could also be an important aspect of force coordination revealing not only the effects of task complexity (de Freitas, Krishnan, & Jaric, 2007; Freitas, Krishnan, & Jaric, 2007), but also the specific aspects of impairment of hand function associated with neurological diseases (Krishnan, de Freitas, & Jaric, 2008; Krishnan & Jaric, 2008; Marwaha, Hall, Knight, & Jaric, 2006).

Although a number of studies implicitly refer to certain tasks as being "more complex" than others are, the relationship between the task complexity and G-L coordination in manipulation activities remains under-explored. In the further text, we will focus on two of the most often manipulated aspects of complexity of the manipulation tasks: the rate of force change and symmetry of bimanual actions.

The rate of force change has been manipulated through increased frequency of the repetitive manipulative actions, such as vertical shaking of a hand-held object (Flanagan & Wing, 1995; Zatsiorsky et al., 2005), or exerting a sinusoidal static L against an externally fixed device (de Freitas et al., 2007; Jaric, Russell, Collins, & Marwaha, 2005). However, the findings have been partly inconsistent. Namely, while the majority of studies demonstrated a frequency associated decrease in the discussed G-L coordination (Flanagan & Wing, 1995; Zatsiorsky et al., 2005), some also suggested in general a stable G and L pattern within a relatively wide range of frequencies (Blank et al., 2001; Jaric et al., 2006). From the perspective of a number of motor control theories and models, the later finding could be considered as surprising. Namely, an increase in the rate of change of muscle force is inevitably associated with increased movement speed and frequency. Hence high frequency tasks has been consistently considered as an important factor that increases the movement complexity of a variety of tasks and, therefore, leads to the deterioration of both task performance and movement coordination (Fitts, 1954; J. A. Kelso, 1984).

In addition to different frequencies, a number of daily activities require bimanual actions of two hands that can be either similar (e.g., clapping hands, lifting bulky objects) or dissimilar (opening jars, playing guitar, eating with fork and knife). In addition to controlling each hand separately, the actions of two hands also need to be mutually coordinated in both similar (Bracewell, Wing, Soper, & Clark, 2003; Jaric, Russell et al., 2005; White, Dowling, Bracewell, & Diedrichsen, 2008) and dissimilar tasks (Scholz & Latash, 1998; Serrien & Wiesendanger, 2001a, 2001b, 2001c). There is a large body of literature suggesting that the symmetric tasks are easier to perform than the asymmetric ones (Haken, Kelso, & Bunz, 1985; J. A.

Kelso, 1984; Sternad, Amazeen, & Turvey, 1996). If nonsimilar actions of two hands need to be simultaneously performed, "assimilation effects" are usually observed. Specifically, movement onsets, durations, and end times tend to be similar when simultaneously grasping targets of different sizes or at different locations (Jackson, Jackson, & Kritikos, 1999; J. A. Kelso, Southard, & Goodman, 1979) and a similar assimilation of forces has been observed when two hands simultaneously exert different static forces (Rinkenauer, Ulrich, & Wing, 2001; Steglich, Heuer, Spijkers, & Kleinsorge, 1999). This phenomenon becomes more prominent with an increase in movement speed (Sherwood, 2004; Swinnen, Walter, Serrien, & Vandendriessche, 1992). Therefore, strong interference between two hands and, in particular, the assimilation effects suggest that a common control (i.e., "bimanual controller") overcomes separate unimanual controllers of two arms (Li, Levin, Forner-Cordero, & Swinnen, 2005; Spijkers & Heuer, 1995). The interlimb interference of G has also been often demonstrated. For example, pressing the bottom of a hand-held object with another hand is associated with a synchronized decrease in G of the holding hand (Scholz & Latash, 1998). A change of G caused either by a voluntary action (Serrien & Wiesendanger, 2001a) or by an unexpected perturbation (Ohki & Johansson, 1999) applied on another hand is partly transferred to G of the holding hand (Blakemore, Goodbody, & Wolpert, 1998).

The material presented in the previous paragraphs suggests that the nonsimilar bimanual actions are not only more complex to control and perform, but also that a higher complexity leads to an increased role of the common central command (i.e., bimanual control) relative to the individual control of two hands. Probably the most notorious example of this phenomenon could be the inevitable switch from "anti-phase" to "in-phase" bimanual tapping associated with an increase in the tapping frequency (J. A. S. Kelso, 1981). It has been recently shown that switching from uni- to bimanual task of producing a prescribed level of total force with a redundant set of fingers is associated with a disappearance of the within-a-hand force stabilizing synergy, while a bimanual synergy is created instead (Gorniak, Zatsiorsky, & Latash, 2007). Therefore, one could assume that an increase in complexity of bimanual manipulation task would be associated with a relatively higher level of coupling of interlimb (i.e., between either G or L of two hands) than within-limb forces (G and L of each hand separately).

To explore the effect of the task complexity on both the task performance and force coordination in bimanual manipulation tasks, we designed an experiment based on static exertion of oscillatory L where we manipulated frequency and symmetry conditions. Since the movement direction and amplitude could be separately controlled at both the behavioral and neural level (Desmurget, Grafton, Vindras, Grea, & Turner, 2003; Fu, Suarez, & Ebner, 1993; Krakauer et al., 2004), we manipulated the L symmetry by manipulating L magnitude and direction of each hand. First, we hypothesized that both an increase in task frequency and changing from symmetric to asymmetric tasks would be associated with a decrease in overall force coordination. Second, we hypothesized that the decrease in force coordination would be more prominent in within-limb than in interlimb force pairs. The expected findings could be of importance for understanding bimanual coordination in general, as well as for future evaluation of hand function in various clinical populations.

Methods

Participants

Fourteen healthy adults (seven males and seven females aged 23–33 years) voluntarily participated in this study. The experimental procedure was approved by the Institutional Review Board of University of Delaware and the participants provided their informed consent in accordance to the Declaration of Helsinki. All participants were right hand dominant, as assessed by the Edinburgh Inventory (Oldfield, 1971).

Experimental Device

The experimental device consisted of two identical externally fixed handles covered by rubber (Figure 1). Our recent experiments suggest the coefficient of friction for the applied precision grip of about 1.7. The handles had an aperture of 3 cm and were positioned 13 cm apart that could roughly correspond, respectively, to the size of tool handles and the distance of two simultaneously manipulated objects in daily life, respectively. They were mounted on a T-profile attached to the table, with adjustable height and orientation. A force transducer (miniature single-axis strain-gauge load cells WMC-50, Interface Inc.) fixed in the middle of the handle recorded the compression force (Fc) exerted laterally by the tip of the thumb. Another multiaxes force transducer positioned below the handle (Mini40, ATI, Apex, NC) recorded all

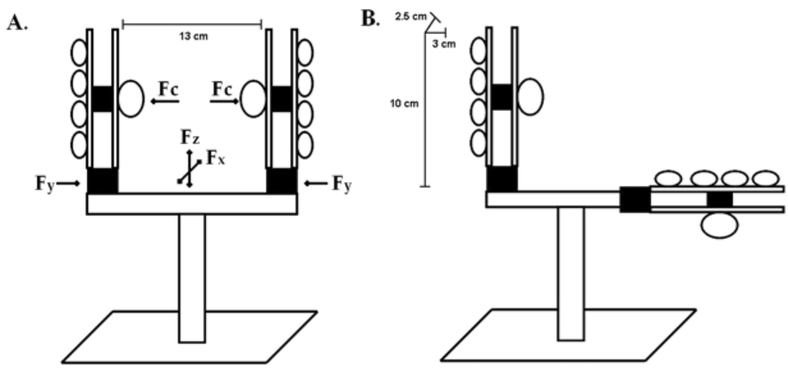

Figure 1 — Schematic illustrations of the device consisting of two handles that are mounted on a height adjustable T-profile attached to the table. The circles illustrate the position of the tips of the fingers and the thumb applying a precision grip against the handles. The single axis force transducers positioned within the handles record both the right and left compression force (Fc), while the multiaxis force transducers positioned below the handles record all three components of the applied forces. Different positioning of the handles allows for exerting L of either different amplitude (A) or direction (B) by two hands.

three components of the force applied against it. Grip force (G) was calculated as the average of orthogonal forces applied against two sides of each handle by recording Fc (from the single axis transducer) and Fy (the horizontal force component from the multiaxes transducer that assess the force exerted medially by the tips of the fingers). Specifically, the grip force was calculated as $G = (|Fc|+(|Fc-Fy|))/2$. Load force (L) was calculated from the vectorial sum of the vertical (Fz) and horizontal (Fx) component providing the total tangential force that could have caused slippage if G were insufficient to prevent it (de Freitas et al., 2007). Pilot testing suggested that the changes in digits positions were restricted by the dimensions of the handle and that they did not affect the measured G. Finally, note that L was used for the assessment of G-L coordination, while Fz was used both for providing the visual feedback and for calculating the task performance variables.

Experimental Procedure

The device was fixed in front of the participant assuming a comfortable standing position, while the height was individually adjusted to allow the upper arm to be in a vertical position, elbow at approximately 90° of flexion, and forearms in midprone positions. The handles were grasped "comfortably" by the tips of the digits applying, therefore, the precision grip. The procedure started with cleaning the tips of the fingers and the thumb, as well as of the surfaces of the handle using an alcohol swab. Thereafter, the maximum voluntary G for each hand was recorded under the instruction to squeeze the handle of the device as hard as possible. A total of three trials were performed for each hand and the maximum value was used for further calculations. According to our previous studies (Jaric et al., 2006; Jaric, Knight et al., 2005), either 10% or 20% of the recorded maximum G of the weaker hand was used in further experiment as the prescribed maximum Fz since, prolonged tasks requiring L below 20% of the maximum G were not expected to cause fatigue.

Finally, the participants were tested on bimanual oscillation tasks performed isometrically. They were instructed to exert a sinusoidal L along the handles by pulling them in the prescribed directions using both hands simultaneously. The computer monitor placed in front of the participant displayed the prescribed maximum and minimum Fz, as well as the current value of Fz for each hand separately. In particular, while one horizontal line (or vertical line in case of *direction experiment*—see further text for details) depicted the individually selected level of Fz maximum, another depicted the minimum Fz level set at 1.5 N. The rationale for setting minimum Fz above zero was to avoid the tested tasks to be "bidirectional". Namely, even a weak and brief Fz exerted in the opposite direction is associated with a remarkable deterioration of force coordination (de Freitas et al., 2007; Jaric, Russell et al., 2005). The exerted force was paced by a metronome set at either 1 Hz or 2.66 Hz. Based on our previous studies, the exerted force pattern was expected to fairly correspond to a sinusoidal pattern, while the selected frequencies corresponded to either comfortable or exceptionally high ones, respectively (Jaric et al., 2006; Jaric, Knight et al., 2005). Note that the participants were asked to focus on exerting force in the prescribed direction (i.e., Fz) and that the same force was used to provide the visual feedback. However, since the force exertion inevitably diverted from the prescribed direction, L (i.e., the total tangential force that corresponds to the vectorial sum of Fz and Fx) was used for calculating the indices of force coordination. In addition, whenever Fx exceeded 50% of the maximum value of Fz, the trials were discarded. Note also that G was not mentioned throughout entire experimental procedure.

Two separate experiments were performed on consecutive days in random sequence. Each one was preceded by 15 min of practice to familiarize the participants not only with the force exertion per se, but also with utilizing the visual feedback regarding the individual forces of two hands provided through two separate signals. Thereafter, four consecutive trials of each of the total number of eight tasks were performed in randomized order (i.e., four tasks at each of two frequencies; see further text for details). The first trial was considered as practice and the following three consecutive trials were recorded for further analysis. The rest between consecutive trials was about 15 s, and about 1 min between the tasks and fatigue was never an issue.

Amplitude Experiment

The amplitude experiment was performed with the handles positioned vertically (see left panel of Figure 1 for illustration) requiring Fz to be exerted vertically upward in all trials. In two "symmetric tasks" the maximum Fz for both hands was set either to 10% or to 20% of maximum G. In two "asymmetric tasks" the maximum Fz was set either to 10% of maximum G for the left and 20% maximum G for the right hand, or 20% of maximum G for the left and 10% maximum G for the right hand.

Direction Experiment

In the direction experiment, Fz was set to 10% of maximum G for both hands in all trials. However, Fz direction was manipulated by changing the orientation of the handles either together or each one separately (see right panel of Figure 1 for illustration). In two "symmetric tasks" the handles' orientation was either vertical or horizontal, requiring Fz to be exerted by pulling them vertically upward or horizontally outward, respectively. In two "asymmetric tasks" the handles' orientation was either set to horizontal for the left and vertical for the right hand, or horizontal for the right and vertical for the left hand.

Data Analysis

G and L signals were A/D converted and recorded at a sampling rate of 200 Hz. Custom-made LabVIEW (National Instruments, Austin, Texas) routines were used for data acquisition and processing. The signals were low-pass filtered at 10 Hz with a fourth order (zero phase lag) Butterworth filter. The individual trials lasted 10 s. The first 4 s of each trial were considered as a time period needed to adjust to both the prescribed frequency and the prescribed force peaks, while the last second could be affected by preparation for the trial termination. Therefore, only the 5 s recording in between were analyzed (de Freitas et al., 2007; Krishnan & Jaric, 2008).

Two groups of dependent variables were selected. To assess the task performance (i.e., the ability to exert the instructed pattern Fz) the variable error (VE; the average of the standard deviations of Fz maxima and minima), constant error (CE; the difference between the observed and the prescribed levels of FZ peaks), and peak-to-peak amplitude of the exerted Fz were calculated. To assess the force coordination (i.e., the relationship between the temporal profiles of G and L) we analyzed G scaling through G/L ratio calculated from the averaged G and L (Flanagan & Wing, 1993; Johansson & Westling, 1984). Namely, we avoided averaging G/L ratio because of occasionally zeros of L that provided the singularity of the calculated function. We also assessed the force coupling by the cross correlation functions among the G and L temporal profiles of two hands. However, in line with a number of previous experiments (Blakemore et al., 1998; Blank et al., 2001; Zatsiorsky et al., 2005), the time lags both between the within-limb (G and L) and interlimb forces (G-G and L-L) proved to be predominantly within the range of ± 10 ms. A preliminary statistical analysis revealed no effect of L asymmetry and frequency on them. Therefore, the correlation coefficient between the forces was taken for further analysis instead (Flanagan & Wing, 1995; Jaric et al., 2006; Nowak & Hermsdorfer, 2002). In line with previous studies, a high force coordination was expected to be revealed by both a low G/L ratio and a high coupling (Flanagan & Wing, 1995; Jaric, Knight et al., 2005; Zatsiorsky et al., 2005).

The value of each dependent variable was averaged across three trials of each hand before the statistical analysis. Coefficients of correlation were Z-transformed before the averaging.

Statistical analysis

Two independent variables were manipulated—L asymmetry (either magnitude or direction) and L frequency. In the first step of the statistical analysis, we separately tested the effect of hand (left vs. right) and the manipulated force (10% vs. 20% of maximum G in the amplitude experiment, and horizontal vs. vertical force in the direction experiment) on each variable. The only significant difference was found regarding VE of the direction experiment. Specifically, VE was somewhat higher in the left (i.e., the nondominant) than in the right hand, as well as in the horizontal than in vertical force exertion. Since we were not interested in lateral differences, we decided to simplify the statistical analysis by averaging the data across the hands. The same was done with the force coordination variables across the force conditions (i.e., two amplitudes and two force directions in the amplitude and direction experiment, respectively). Thereafter, repeated-measures ANOVA were used to assess the main effects on each variable separately. In particular, 3-way ANOVA were used to assess the main effects of "force condition" (10% vs. 20% of maximum G in the amplitude experiment, and horizontal vs. vertical force in the direction experiment), "frequency" (1 Hz vs. 2.66 Hz) and "symmetry" (symmetric vs. asymmetric tasks) on the task performance variables of each experiment separately. Regarding the force coordination variables, 2-way ANOVA was used to test the main effects of "frequency" and "symmetry" on G/L ratio, while a 3-way ANOVA evaluated the main effects of the "force pair" (GL vs. GG vs. LL; GL depicting within-limb, and GG and LL depicting the interlimb coordination), "frequency" and "symmetry". The Bonferroni post hoc correction was applied wherever necessary and the p-value was set to 0.05. Statistical analysis was performed in SPSS 10 for Windows (SPSS Inc., Chicago, USA).

Results

Amplitude Experiment

Figure 2A shows the force profiles obtained from a representative participant in the amplitude experiment. While the left panel illustrates the force production of the symmetric task (10% of G maximum) performed at the low frequency, the right side panel shows the data observed from the same participant in the asymmetric task performed at high frequency. Visual inspection suggests less consistent L peaks (i.e., higher VE) and somewhat less consistent timing of all four forces in the asymmetric task performed at high frequency.

Regarding the task performance variables, the absolute values of constant errors (CE; calculated separately for Fz maxima and minima; data not depicted) were

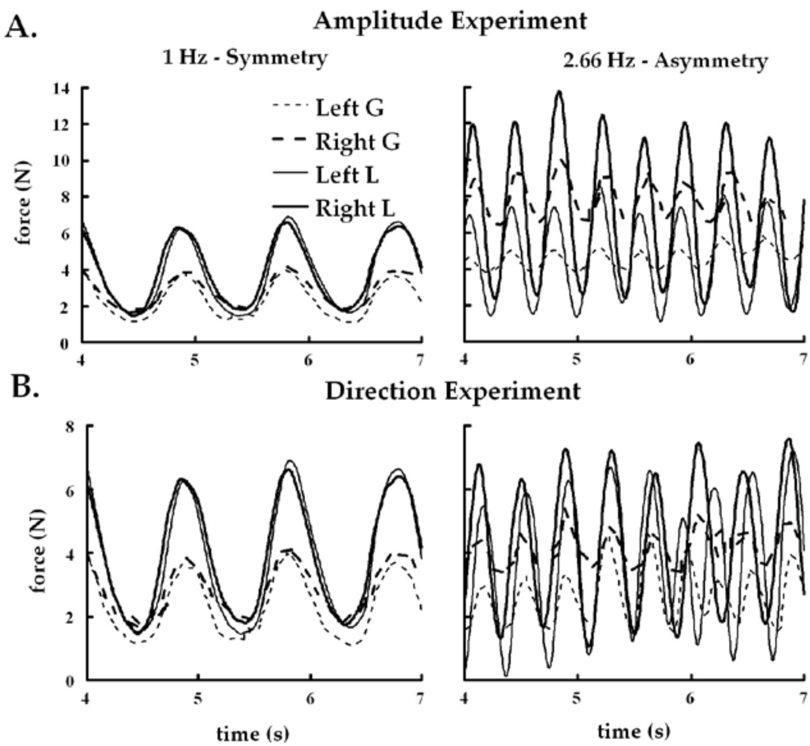

Figure 2 — Time series of the left and right hand of a representative participant exerting G and L in a symmetric task at 1 Hz (left hand panel) and asymmetric task at 2.66 Hz (right hand panel) in the amplitude experiment (A) and direction experiment (B). For better visualization, the figure shows only three out of five seconds of the processed data.

relatively small, ranging between 0.002 N and 1.1 N. In addition to the expected difference in force amplitudes observed between 10% and 20% of maximum G ($F_{(1,13)}$ =464.04, $p < .001$), 3-way repeated-measures ANOVA (force condition × frequency × symmetry) reveals a significant force condition × symmetry interaction ($F_{(1,13)}$=18.05, $p < .001$; Figure 3A). Specifically, in asymmetric tasks the lower level of the prescribed force (i.e., 10% of maximum G in left and right hand) was higher when the opposite hand was exerting 20% of maximum G. Similarly, the higher force (20% of maximum G in left and right hand) was lower when the opposite

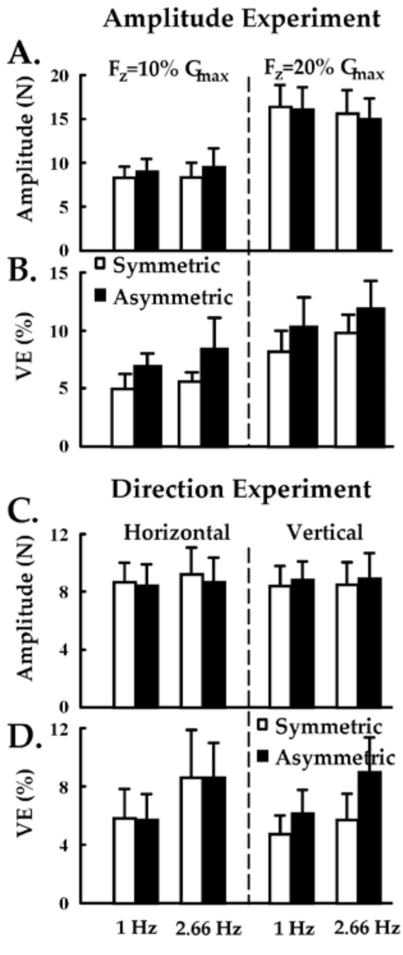

Figure 3 — Task performance of the amplitude experiment (A and B) and direction experiment (C and D) depicted through Fz amplitude and variable errors for different symmetry and frequency conditions (data averaged across the participants depicted by means with *SD* error bars across the participants).

hand was exerting 10% of maximum G. Therefore, the exertion of Fz of each hand partly depended on the level of Fz of another hand, which has often been referred to as "bimanual assimilation". VE was higher at the higher forces ($F_{(1,13)}$=145.44, $p < .001$), at higher frequency ($F_{(1,13)}$=9.45, $p < .01$), and in asymmetric tasks ($F_{(1,13)}$=41.72, $p < .001$), with no interactions (Figure 3B).

Regarding the force coordination variables averaged across the participants, G/L ratio revealed neither the main effects of symmetry and frequency, nor a significant interaction (Figure 4A). Figure 4B depicts median values of the correlation

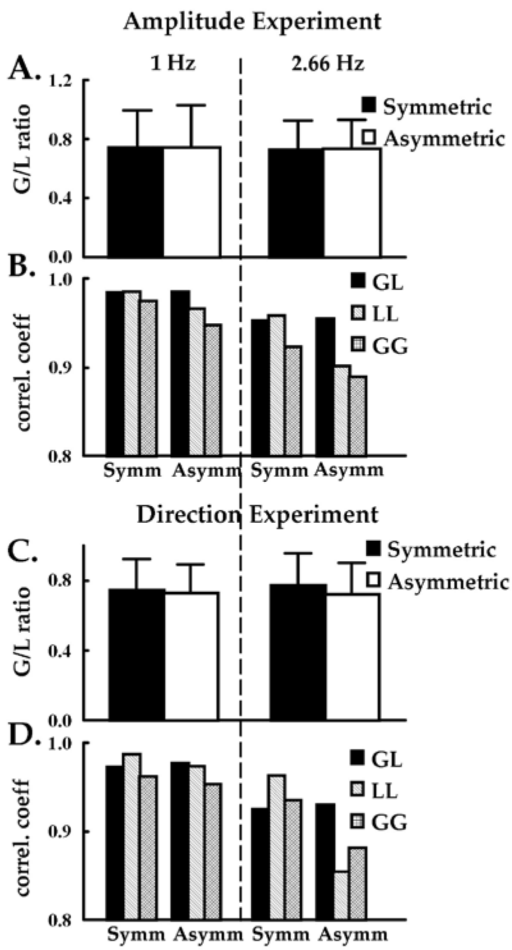

Figure 4 — G/L ratio (means with *SD* error bars; panels A & C) and within-limb (GL) and interlimb (LL and GG) force coordination depicted by median correlation coefficients (median values; panels B & D) observed from the amplitude experiment and direction experiment (data averaged across the participants).

coefficients observed among different force pairs. Note that GL correlations reveal the coupling of the within-limb force pairs (i.e., G and L within each hand), while GG and LL correlations reveal the coupling of the interlimb force pairs. The results showed the main effects of force pairs ($F_{(2,26)}$=32.9, $p < .001$) where GG coupling was significantly lower than GL coupling. Coupling of all three force pairs was also lower in the asymmetric than in symmetric tasks ($F_{(1,13)}$=42.2, $p < .001$), as well as in the trials performed at higher than in the trials performed at the lower frequency ($F_{(1,13)}$=62.58, $p < .001$). Of particular importance for this study could be the force pair × symmetry interaction ($F_{(2,26)}$=43.4, $p < .001$). Namely, the data suggest that changing from the symmetric to asymmetric task is associated with a more prominent deterioration of coupling of the interlimb than of the within-limb force pairs.

Direction Experiment

Figure 2B show the force profiles obtained from a representative participant in the direction experiment. The left side panel illustrates the force profiles of the symmetric task (pulling handles vertically) performed at the low frequency. The right side panel shows the data observed from the same participant in the asymmetric task performed at the high frequency. In addition to the more inconsistent force peaks which should lead to a higher VE, these data also suggest a relatively poor timing of the peaks of all four forces. An inevitable consequence should be a reduced force coupling as assessed by the correlation coefficients calculated among particular force pairs.

The absolute values of constant errors were relatively small, ranging between 0.003 N and 2.34 N. The force amplitudes were fairly consistent across the tasks (Figure 3C). The only significant effect was the direction × symmetry interaction ($F_{(1,13)}$=22.7, $p < .001$) suggesting higher amplitudes in symmetric than in asymmetric tasks in "horizontal" direction, while the opposite effect was recorded in "vertical" direction. VE were higher at low than at high frequency ($F_{(1,13)}$=27.1, $p < .001$), as well as in asymmetric than in symmetric tasks, but only in the tasks with forces exerted vertically (direction × symmetry interaction; $F_{(1,13)}$=23.0, $p < .001$). The interaction of all three factors was also significant ($F_{(1,13)}$=6.1, $p < .05$) suggesting that the effect was more prominent at higher frequency.

Figure 4C and 4D show the force coordination variables averaged across the participants. The statistical analysis revealed the main effect of symmetry on G/L ratio ($F_{(1,13)}$=8.2, $p < .05$) with no interactions (Figure 4C). Namely, the symmetric tasks revealed higher G/L ratio than the asymmetric tasks. Figure 4D illustrates median correlation coefficients as indices of force coupling obtained from the within-limb force pairs (GL, averaged across two hands) and interlimb force pairs (GG and LL). Three-way repeated-measures ANOVA (force pair × frequency × symmetry) revealed lower correlation coefficients in asymmetric than in symmetric tasks ($F_{(1,13)}$=48.6, $p < .001$), in tasks performed at higher than at lower frequency ($F_{(1,13)}$=125.1, $p < .001$), and in interlimb than in within-limb force pairs ($F_{(2,26)}$=29.8, $p < .001$). Of particular importance could be a strong force pair × symmetry interaction ($F_{(2,26)}$=83.6, $p < .001$) suggesting that changing from symmetric to asymmetric task affects more interlimb than within-limb coupling. Furthermore, the force pair × frequency interaction ($F_{(2,26)}$=11.3, $p < .001$) suggest that in general the drop in the force coupling is more prominent at high frequency.

Discussion

Within the current study, we explored the effect of the task frequency and symmetry on the force coordination in bimanual static manipulation tasks. In general, most of the data supported the first hypothesis regarding the complexity-associated decrease in force coordination. Regarding the second hypothesis, however, the data mainly contradicted the hypothesized complexity associated decrease in coordination of within-limb forces (i.e., forces "within the hand"), as compared with the coordination of interlimb forces (i.e., coordination of lateral L and G).

Task performance and G/L ratio

Since the task was to match the prescribed levels of the maxima and minima of the oscillatory Fz profiles, we assessed the performance through the variable errors (VE) of Fz peaks, as well as with the peak-to-peak Fz amplitudes. VE increase was associated both with an increase in frequency and with changing from the symmetric to asymmetric tasks. The peak-to-peak Fz of the amplitude experiment also suggested symmetry associated changes that could be explained by interlimb assimilation effect that leads to overshooting lower and undershooting higher Fz targets. Finally, the coupling of within-limb and interlimb forces in both experiments decreased with an increase in frequency, as well as with changing from symmetric to asymmetric task. Therefore, we could conclude that the tasks we subjectively feel as more complex ones (i.e., either the high frequency or asymmetric tasks) are associated with a deteriorated force control, which includes both a reduced task performance (i.e., ability to exert an accurate Fz pattern) and reduced force coordination. An exception could be G/L ratio that remained unaffected by changes in the task. This finding could be somewhat surprising having in mind that G/L ratio, as well as the associated safety margin (Johansson & Westling, 1984) could be a sensitive measure either of the force control per se (Jaric, Knight et al., 2005; Zatsiorsky et al., 2005) or of the deterioration of hand function associated with neurological diseases (Gordon, Ingvarsson, & Forssberg, 1997; Krishnan & Jaric, 2008; Nowak & Hermsdorfer, 2005). We believe that a part of explanation could be based on the static nature of the tested task that involves partly different control mechanisms than the more often tested dynamic tasks (Zatsiorsky et al., 2005). Nevertheless, both the symmetry and frequency of manipulation task could be important factors of manipulation task complexity and, therefore, they should be taken into account in not only in motor control studies, but also in designing both the testing and therapeutic procedures for populations with impaired hand function.

Interlimb and Within-Limb Force Coordination

While the findings discussed within the previous section could be generally considered as expected, the data related to the interlimb and within-limb force coordination might be somewhat surprising. Namely, an increased task complexity is generally expected to lead to a relatively more coordinated action of two limbs. Regarding the task symmetry, when the complexity increases, an "antiphase" (i.e., asymmetric) task that requires two limbs to be separately controlled, tends to spontaneously switch to symmetric one where the control signal (and, therefore, the force pattern) becomes common for two limbs (J. A. Kelso, 1984). However, our data suggest that the increase in task complexity was associated with more prominent deterioration in interlimb than in within-limb coordination. The following paragraphs will present a possible interpretation of the observed phenomena based on two predominantly independent neural control mechanisms employed in interlimb and within-limb force coordination.

Bernstein (1967) suggested a multihierarchical limb control where, when the task complexity increases, the "bimanual controller" takes over the unimanual controllers to reduce the number of separately controlled degrees of freedom (see also (Turvey, 1977)). More specifically, the action of the hypothetical controllers results in creating task specific synergies that represent a neural organization of a multielement system that are designed to improve task performance and share a common input or neural drive, which leads to a stable relationship among these multielements over time (Latash, Scholz, Danion, & Schoner, 2002). This concept explains the tendency for synchronous timing of both discrete and rhythmic bimanual movements and force exertions, as well as spontaneous switching from asymmetric to symmetric bimanual patterns (Diedrichsen, Hazeltine, Nurss, & Ivry, 2003; J. A. Kelso, 1984; J. A. S. Kelso, 1981; Rinkenauer et al., 2001; Steglich et al., 1999). Here, we believe that only the coordination of interlimb forces could be a consequence of the above described task specific and *ad hoc* created synergies. According to the above-described basic concept, muscles of both arms could share a common neural input and, therefore, the correlations among all four forces are exceptionally high in symmetric tasks. In asymmetric tasks, at least the interlimb L muscles could be separately controlled. Therefore, the indices of interlimb force coordination deteriorate but, because of the involvement of bimanual controller (Spijkers & Heuer, 1995) and/or neural "crosstalk" (Marteniuk, Mackenzie, & Baba, 1984), to a lesser extent.

While the control of the movement amplitude and direction (presumably responsible for controlling interlimb L) could be coded primarily at the level of single cells and cell populations of the superior motor area and primary cortex (Fu et al., 1993), coordination of the within-limb forces (i.e., G and L of each hand separately) could be mainly located deeper within the brain structures and, therefore, demonstrate different properties. In particular, G modulation with respect to the ongoing changes in L could be partly reflex driven (Cole & Abbs, 1988; Johansson & Westling, 1988; White et al., 2008) and, therefore, cannot be voluntarily overcome (Davidson, Wolpert, Scott, & Flanagan, 2005; Flanagan, Vetter, Johansson, & Wolpert, 2003). Due to a partly reflex nature, when either initiating the task against unknown object (Cole & Abbs, 1988; Johansson & Westling, 1987), or reacting to unexpected perturbation (Blakemore et al., 1998; Johansson, Hger, & Backstrom, 1992; Johansson & Westling, 1988), or performing consecutive changes in L direction (de Freitas et al., 2007; Jaric, Russell et al., 2005), the reactive nature of the coordinative neural mechanism requires a certain time to establish a close coupling of G and L. When acting against a known hand-held object or performing a continuous manipulation (such as in the current study) using the "predictive mechanisms" (Flanagan & Wing, 1995; Jaric, Russell et al., 2005), the within-limb coordination is based on setting a steady G/L ratio adjusted to the acting friction by a certain safety margin (Johansson & Westling, 1984) which is inevitably based on a stable and exceptionally high level of G and L coupling. Due to their reflex nature, the within-limb coordination of G and L of each hand in the tested continuous task remains mainly preserved across the tasks of different complexity (Jaric et al., 2006). Therefore, the considerably decoupled interlimb forces in the tested asymmetric tasks can only mildly affect the predominantly reflex driven and stable within-limb coordination of G and L of each hand, possibly through a multilevel crosstalk (Marteniuk et al., 1984).

The present study revealed two potentially important findings. First, both the frequency and symmetry of bimanual manipulation tasks could be considered as factors of the task complexity that lead to deteriorated force coordination. Since the assessment of force coordination in various manipulation tasks have increasingly become an important approach in studying and evaluating hand function in both healthy and clinical population, this finding should be taken into account when designing future testing protocol. Second, the increase in complexity is associated with more prominent deterioration in interlimb (i.e., between two lateral G and L) than within-limb coordination (between G and L of each hand). This finding could be interpreted by two partly independent control mechanisms that do not compete with each other, such as in the competing mechanisms that cause switching among different rhythmic bimanual patterns (J. A. Kelso, 1984), bimanual holding (Scholz & Latash, 1998), or between the within-hand and across-hand synergies of finger force production (Gorniak et al., 2007). Future research could extend our approach to other manipulation tasks that could be based on partly different mechanisms of G control, such as the free movement tasks and the tasks based on reactive control (Bracewell et al., 2003; White et al., 2008; Zatsiorsky et al., 2005), as well as on a variety of unimanual and bimanual grasping techniques that all seem to provide elaborate coordination of within-limb G and L (de Freitas & Jaric, 2009; Freitas et al., 2007). Potential role of changes in friction coefficients of individual fingers and their synergies could also deserve attention (Zatsiorsky, Li, & Latash, 1998).

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