

Plane of Motion Mediates the Coalition of Constraints in Rhythmic Bimanual Coordination

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ABSTRACT. The authors hypothesized that the modulation of coordinative stability and accuracy caused by the coalition of egocentric (neuromuscular) and allocentric (directional) constraints varies depending on the plane of motion in which coordination patterns are performed. Participants ($N = 7$) produced rhythmic bimanual movements of the hands in the sagittal plane (i.e., up-and-down oscillations resulting from flexion–extension of their wrists). The timing of activation of muscle groups, direction of movements, visual feedback, and across-trial movement frequency were manipulated. Results showed that both the egocentric and the allocentric constraints modulated pattern stability and accuracy. However, the allocentric constraint played a dominant role over the egocentric. The removal of vision only slightly destabilized movements, regardless of the effects of directional and (neuro)muscular constraints. The results of the present study hint at considering the plane in which coordination is performed as a mediator of the coalition of egocentric and allocentric constraints that modulates coordinative stability of rhythmic bimanual coordination.

Key words: allocentric constraint, coordination dynamics, egocentric constraint, perception, vision

How do multiple constraints, ranging from high-level cognitive-perceptual to low-level (neuro)muscular, contribute to the emergence of coordinated behavior? Among the great variety of experimental studies in which researchers have used coordination dynamics as a theoretical framework to investigate that question, rhythmic bimanual coordination remains a favorite. That simple experimental paradigm, introduced more than 20 years ago (Haken, Kelso, & Bunz, 1985; Kelso, 1981, 1984), has provided human movement science with new ways to understand processes that blend motor, perceptual, and cognitive functions (see Kelso, 1995; Swinnen, 2002; Swinnen & Wenderoth, 2004, for reviews). However, a debate persists with respect to the nature (cooperative, competitive, or both) of the interaction between (neuro)muscular, visual,

directional, or even intentional and attentional constraints (e.g., Carson, 2004; Lee, Blandin, & Proteau, 1996; Mechsner, 2004a, 2004b; Oullier, Bardy, Stoffregen, & Bootsma, 2004; Temprado, Zanone, Monno, & Laurent, 1999). Although in recent studies, investigators have favored the hypothesis that a coalition of constraints modulates behavioral stability (e.g., Li, Levin, Carson, & Swinnen, 2004; Oullier, de Guzman, Jantzen, & Kelso, 2003; Oullier, Jantzen, Steinberg, & Kelso, 2005; for an alternative point of view, see Mechsner, 2004b), a coherent framework is still lacking, especially regarding the conditions under which such constraints are influential (Salesse, Temprado, & Swinnen, 2005; Serrien, Bogaerts, Suy, & Swinnen, 1999; Temprado & Salesse, 2004; Temprado, Swinnen, Carson, Tourment, & Laurent, 2003).

Since Kelso's seminal studies (1981, 1984), bimanual coordination dynamics performed in the transverse plane of motion¹ has been addressed in an abundant body of literature (see Kelso, 1995, for a review). It has been shown that when movements are performed in that plane, constraints imposed by the coactivation of homologous and nonhomologous muscles predominantly (if not exclusively) affect both stability and accuracy of bimanual coordination patterns. More specifically, mirror symmetrical movements with respect to body midline, resulting from simultaneous activation of homologous muscles, are more stable and accurate than asymmetrical ones, that is, movements requiring simultaneous activation of nonhomologous muscles and leading one limb to move toward the body midline while the

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other moves away from it (e.g., Li et al., 2004; Monno, Chardenon, Temprado, Zanone, & Laurent, 2000; Riek, Carson, & Byblow, 1992). In the literature, such a preference for homologous muscular coupling is currently referred to as the *egocentric constraint* (see Swinnen, 2002; Swinnen, Jardin, Meulenbroek, Dounskaia, & Van den Brandt, 1997; Swinnen et al., 1998).

Most interesting, in the sagittal plane of motion, coordination involving nonhomologous limbs affords quite a different picture. For instance, Baldissera, Cavallari, and Civaschi (1982) studied the coordination of ipsilateral hand and foot movements in which both limb segments moved in either the same (both segments up or down together, i.e., isodirectional) or opposite directions (one segment up and the other down, i.e., nonisodirectional). They showed that nonisodirectional movements were harder to perform. Phase transitions that occurred predominantly from nonisodirectional to isodirectional movements illustrated that effect. In addition to those results, Baldissera and colleagues manipulated forearm posture (e.g., prone or supine position). The implicit assumption underlying that procedure was that inversion of forearm posture would alter the relative timing of the activation of the muscle groups producing the in-phase and the antiphase coordination patterns. Because transitions from nonisodirectional to isodirectional movements were observed regardless of the adopted forearm posture (prone or supine position), Baldissera et al. concluded that the direction of the movements was the determining factor in (de)stabilizing hand-foot coordination. Following the early work of Baldissera et al., other researchers have investigated pattern stability and accuracy in similar hand-foot coordination tasks, with converging results (Carson, Goodman, Kelso, & Elliott, 1995; Salesse & Temprado, 2005; Salesse et al., 2005). Moreover, direction dependence of pattern stability has been reported in other studies on arm-leg (e.g., Jeka & Kelso, 1995; Kelso & Jeka, 1992) or intralimb wrist-elbow coordination (e.g., Buchanan & Kelso, 1993; Kelso, Buchanan, & Wallace, 1991). Those findings suggest that performing coordination in the sagittal plane of motion rather than coordinating heterogeneous limb components may result in the dominance of directional constraints. The marked preference for executing isodirectional movements more accurately and consistently than nonisodirectional ones in the sagittal plane of motion is referred to as the *allocentric constraint* (Swinnen, 2002; Swinnen et al., 1997, p. 349; Swinnen et al., 1998).

To date, both egocentric and allocentric constraints have been studied in relative isolation (Swinnen et al., 1997; see Swinnen, 2002, for a review). Furthermore, they have been associated with different limb combinations (upper vs. upper-lower limbs) as well as with different planes of motion (transverse vs. sagittal; Swinnen, 2002). The question therefore remains regarding how the respective contributions of egocentric and allocentric constraints to (bimanual) coordination dynamics may vary depending on the plane of motion in which patterns are executed. To date, in

very few studies has that issue been addressed. One noticeable exception is the research conducted by Serrien et al. (1999). Their participants had to perform circle-drawing tasks in different planes of motion. Their working hypothesis was that the effects of influential constraints on interlimb coordination could be mediated by the plane of motion: the allocentric constraint being dominant in the sagittal plane, the egocentric being dominant in the transverse plane. Serrien and colleagues' results partially confirmed that hypothesis. In both the transverse and the sagittal planes of motion, patterns performed with homologous muscular coupling were always more stable than those performed with nonhomologous muscular coupling, and isodirectional ones were found to be more stable than nonisodirectional ones. Moreover, in the transverse plane of motion, a dominant role of the egocentric constraint and a subordinate role of the allocentric constraint were found. On the other hand, performance in the sagittal plane of motion differed markedly from that in the other planes. More specifically, isodirectional movements proved to be more stable than nonisodirectional ones. Serrien et al. concluded that in their experimental context (i.e., circle-drawing tasks), the sagittal plane of motion was less suitable for assessing the overall role of egocentric and allocentric constraints. The results of a recent study by Temprado et al. (2003, Experiment 3) complemented Serrien and colleagues' findings and provided preliminary evidence that, in the sagittal plane of motion, both egocentric and allocentric constraints contribute to bimanual pattern stability (for similar findings, see Temprado & Swinnen, 2005). The results of that study contrasted with those of Riek et al. (1992) on bimanual coordination (index fingers flexion-extension) performed in the transverse plane of motion. For instance, when they manipulated forearm posture, those authors showed that (neuro)muscular constraints were dominant over directional ones (see also Carson, 1996; Carson, Riek, Smethurst, Párraga, & Byblow, 2000, for a similar conclusion).

Taken together, those findings suggest that changing the plane of motion in which the coordination is performed could modulate the relative contribution of egocentric and allocentric constraints to bimanual coordination dynamics. In the present study, we attempted to test that hypothesis. We required participants to perform rhythmic bimanual coordination in the sagittal plane of motion (i.e., up-and-down movements of the hands resulting from flexion-extension of the wrists). We manipulated the nature of the coactivated muscles groups (i.e., homologous or nonhomologous muscle groups) and the direction of motion (isodirectional and nonisodirectional) so that the effects of egocentric and allocentric constraints were either mutually reinforced or opposed. We hypothesized that in the sagittal plane of motion, performing simultaneous limb movements in either similar (isodirectional) or different directions (nonisodirectional) should stabilize or perturb, respectively, rhythmic bimanual coordination, regardless of the muscle groups coactivated (homologous or nonhomologous).

In addition, we contrasted conditions with and without vision of the moving limbs to assess the role of visual feedback in bimanual coordination in the present context. Indeed, the results of many studies have demonstrated that visual scenes characterized by stimuli moving in the same direction are perceived more consistently and more accurately than are other motion structures (e.g., Bingham, Zaal, Shull, & Collins, 2001; Bogaerts, Buekers, Zaal, & Swinnen, 2003; Temprado & Laurent, 2004). In light of those studies, we expected visual information on the motion of the hands to modulate the stability of the coordination pattern to be performed. We meant by that comparison to address the (visual) principle of isodirectionality as a contributing factor to pattern (de)stabilization in rhythmic coordination (Bogaerts et al., 2003; Salesse & Temprado, 2005; Salesse et al., 2005). If the loss of stability resulting from direction dependence was related to the presence of visual information, then one would expect vision of an isodirectional pattern to stabilize bimanual coordination but vision of a nonisodirectional pattern to be destabilizing.

Method

Participants

Seven right-handed adults (4 women and 3 men) ranging in age from 22 to 30 years ($M = 26$ years) volunteered for participation in the experiment. All participants reported normal or corrected-to-normal vision. Participants were naive to our purpose in the experiment. Each participant filled out written consent forms before the experiment. The experimental protocol received full approval from the local ethics committee.

Apparatus

Participants sat on a multiarticulated coordination apparatus. Their upper limbs were secured on a shaft with a wide Velcro belt, ensuring that movements were restricted to flexion–extension of the hand in the sagittal plane, that is, up-and-down oscillations (Figure 1A). Forearms were supported in a 90° angular position with respect to the upper arm (Figure 1B). The chair made a 30° angle with the vertical axis. Participants had to grab a manipulandum in each hand. The axes of the manipulanda were aligned with the wrist joint. Each manipulandum could rotate within a $\pm 80^\circ$ range, as illustrated in Figure 1B. The large amplitude range allowed participants to have virtually unrestricted movements of their hand in the sagittal plane regardless of the posture required by the experimental design. We recorded hand movements at a sampling frequency of 200 Hz by using linear potentiometers (Spectrol, Ontario, CA, Model 148DXG56S502SP, $\pm 5\%$) placed on the axis of rotation of each manipulandum. An auditory metronome paced the movements; its tones (3.3-kHz square waves, duration = 50 ms) were delivered by a buzzer located in front of the participants.

Procedure

Participants were requested to produce continuous bimanual rhythmic up-and-down movements of the hands.

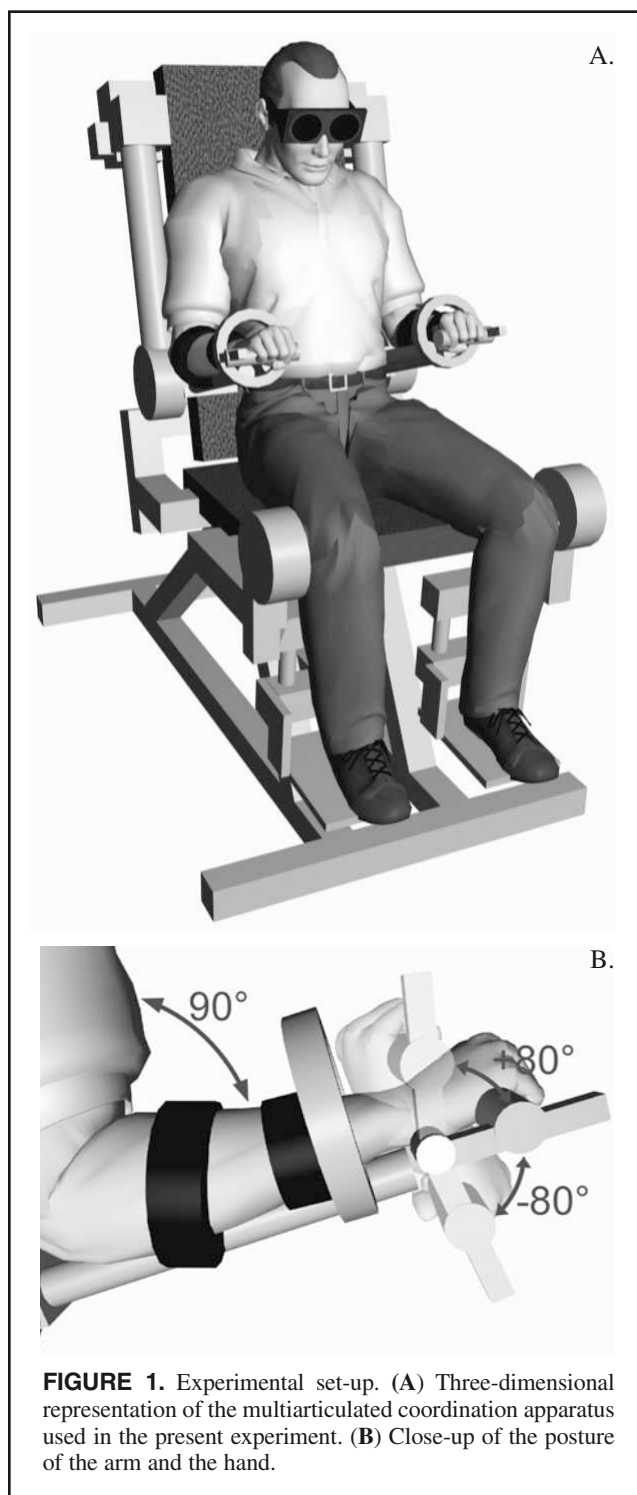


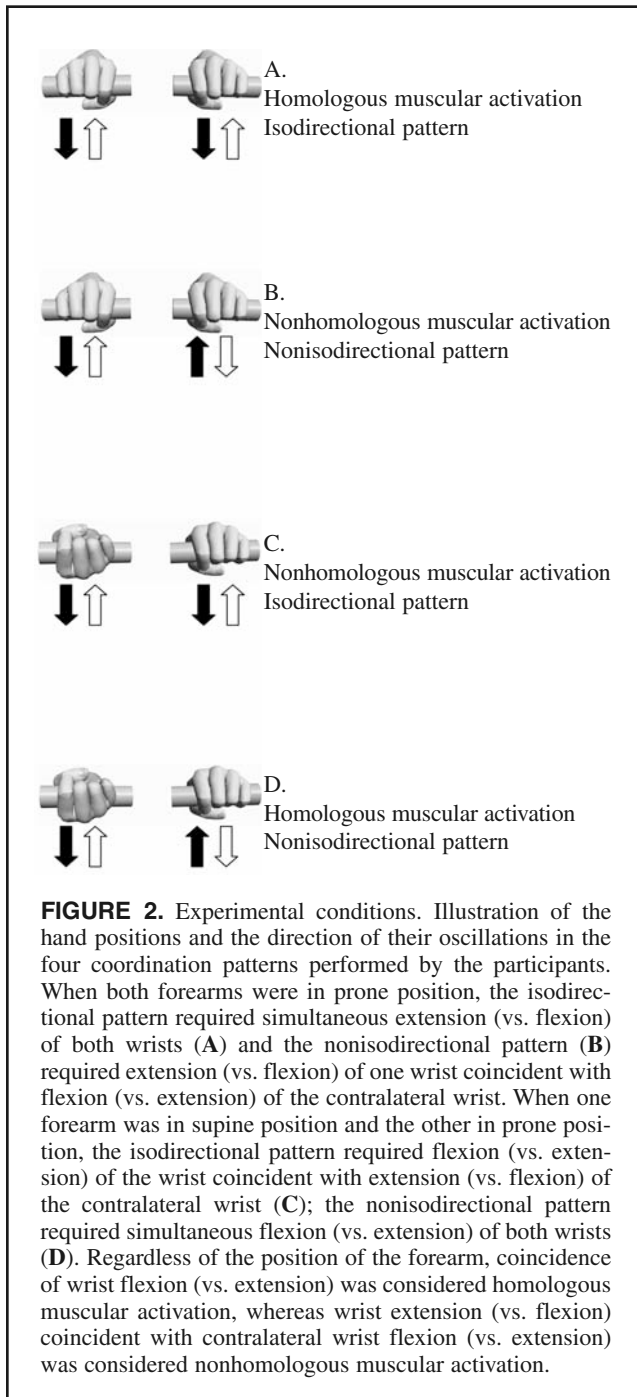
FIGURE 1. Experimental set-up. (A) Three-dimensional representation of the multiarticulated coordination apparatus used in the present experiment. (B) Close-up of the posture of the arm and the hand.

We fully crossed four independent variables in the experiment for a total of 40 different experimental conditions: relative direction of movement (isodirectional vs. nonisodirectional), coactivation of muscle groups (homologous vs. nonhomologous), visual feedback (vision vs. no vision), and movement frequency (1.0, 1.5, 2.0, 2.5, and 3.0 Hz).

1. We manipulated the relative direction of movements by asking participants to perform either isodirectional

movements (both hands moved upward and downward simultaneously) or nonisodirectional movements (one hand moved upward and the other downward, and vice versa). That condition is referred to in the analysis as the *effect of direction* (see Figure 2).

2. We manipulated the coactivation of (non)homologous muscle groups by asking participants to grab the manipulandum either with both forearms in prone posture² or with one forearm prone while the other one was supine. When both forearms were in the prone position, the isodirectional pattern required the simultaneous activation of homologous muscle



groups, whereas the nonisodirectional pattern required the simultaneous activation of nonhomologous muscle groups. When forearms were placed in dissimilar positions (one forearm prone and the other one supine), the isodirectional pattern required the simultaneous activation of nonhomologous muscle groups, whereas the nonisodirectional pattern required the simultaneous activation of homologous muscle groups (see Figure 2). Any effect of the muscle groups involved in the production of coordination patterns (homologous vs. nonhomologous) is referred to in the analysis as a *muscular activation effect*. During conditions in which forearm postures were dissimilar (i.e., prone or supine), half the trials were performed with the right forearm supine, whereas the other half were performed with the left one supine.

3. We manipulated visual information by allowing participants to see (vision) or not see (no vision) the movements of their hands. That effect is referred to in the analysis as *vision*. In the so-called vision conditions, participants wore transparent goggles; they were instructed to look at their moving hands. The goggles were completely opaque in the no-vision conditions.

4. Movement frequency remained constant within a trial but changed randomly from one trial to another. We tested five frequencies: 1.0, 1.5, 2.0, 2.5, and 3.0 Hz. We refer to that effect as *frequency* in the analysis.

Before each trial, participants were given instructions regarding the forearm posture to adopt and the relative direction of movement. We told them to coordinate their hands as accurately and continuously as possible with respect to the direction of movement and the pacing frequency. We instructed them not to resist the pattern change (i.e., the so-called do not intervene instruction; see Kelso, 1984), that is, to maintain the initial coordination pattern unless they felt that switching to another pattern would allow the task to be performed more comfortably at the prevailing frequency.

Each experimental trial lasted 15 s and 8 trials per condition were performed, for a total of 320 trials. Participants were given a 10-s rest period between each trial and a break of 10-min every 80 trials.

Data Analysis

A previously performed fast Fourier transform- (FFT) based analysis on the raw data revealed that the frequency spectrum was essentially located below 4 Hz. Consequently, we filtered data with a second-order dual-pass Butterworth filter with an 8-Hz cutoff frequency. After the filtering process, data were centered around zero; we normalized those data in a $-1,1$ range before computing the dependent variables (Mottet & Bootsma, 1999).

We computed the cycle-by-cycle effective movement frequency (averaged across both hands) for each trial, together with a frequency deviation score. That score reflects the absolute difference between the average within-trial effective frequency and that of the metronome. For the analysis

of that variable, we chose a $p < .2$ level of significance to prevent a Type II error (Abdi, 1987).

The relative phase between the oscillations of the right and the left hands served as the measure of bimanual coordination. We computed point estimate relative phase with the right hand as the reference by using a peak-peaking algorithm (e.g., Zanone & Kelso, 1992).

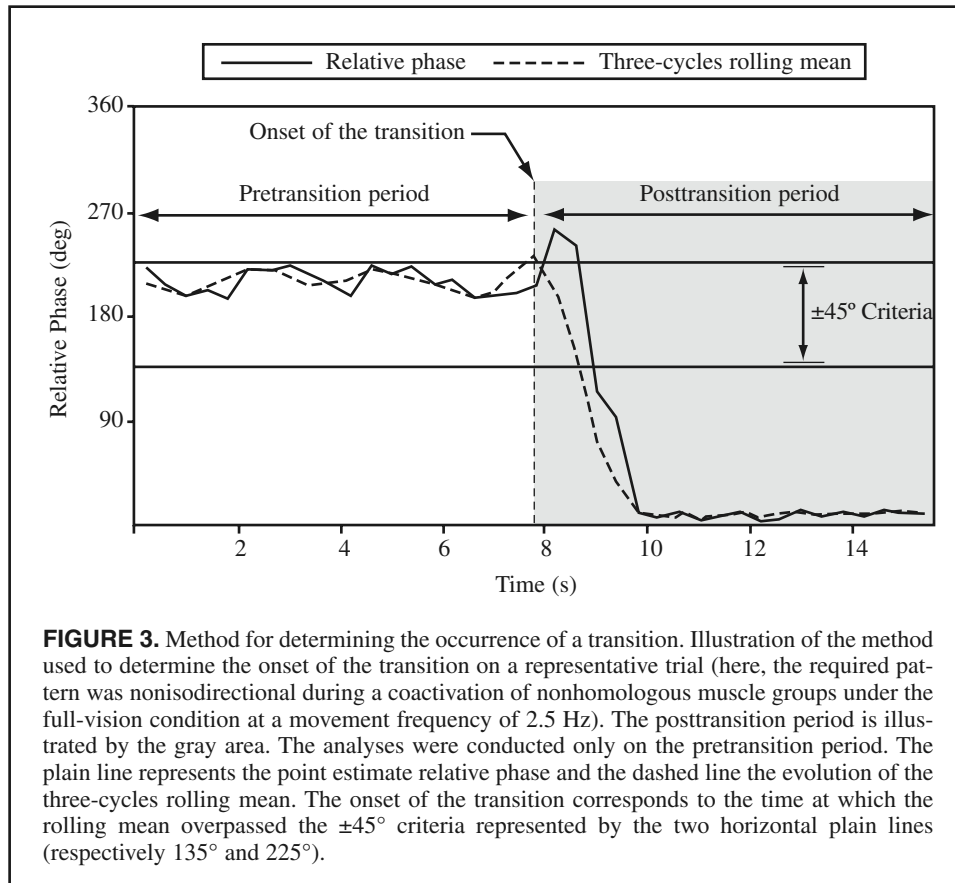
We assessed the stability of the coordination patterns by computing the number of phase transitions, the time to transition, and the standard deviation (*SD*) of relative phase in the pretransition period. To identify phase transitions (i.e., an abrupt switch from one pattern to another), we used a specific visualization process via a customized graphic interface (see Figure 3 for an illustration of the procedure). Thanks to the interface, the experimenter was informed when the mean value of three consecutive cycles of relative phase was leaving a $\pm 45^\circ$ range around the required phase to be performed. We then set position cursors at the last relative phase value within that range. That value defined the end of the pretransition period, that is, just before the required relative phase shifted to another stable phase relation. The procedure therefore allowed the experimenter to separate pre- and posttransition regions (for a similar method, see Carson et al., 1995).

Each participant performed each of the 40 different conditions eight times. Thus, for each participant, in each condition, we summed (from 0 to 8) the number of phase transitions.

Then, we transformed that number into a percentage, which varied from 0% to 100%. We then transformed the percentage of phase transitions by using a root square arcsine transform to ensure both the homogeneity of the variance and the normality of the error distribution (Abdi, 1987).

We defined *time to transition* as the time between the beginning of one trial and the end of the pretransition period. For trials in which no transition was observed, we set that value to the total duration of the trial (i.e., 15 s; see Monno et al., 2000, for a similar method). We assessed variability of coordination patterns by computing the *SD* of relative phase. Finally, we used the absolute error of relative phase as an index of accuracy of bimanual coordination. The absolute error is the unsigned difference between the mean relative phase and the required pattern.

We calculated time to transition, *SD*, and absolute error of relative phase for pretransition periods. We tested the values of the absolute error of relative phase and the corresponding variability for normal distribution. We excluded from the variance analysis trials that did not satisfy the criteria of uniformity (using a normal law with a 95% confidence interval; Abdi, 1987) and trials whose values initially corresponded to a posttransition value of reference. Using that method, we rejected 43 trials (out of 2,240). We performed a 2 (direction) \times 2 (muscular activation) \times 2 (vision) \times 5 (frequency) two-way analysis of variance (ANOVA) with repeated measures on the transformed values of percentage



of phase transition, time to transition, *SD*, and absolute error of relative phase. The chosen level of significance was $p < .05$ (Abdi, 1987). We performed post hoc decompositions of interactions by means of Newman–Keuls tests. Finally, we computed the intensity effects (*IE*) indicating the proportion of variance in the dependent variable accounted for by the independent variable by using ω^2 (Winer, Brown, & Michels, 1991).³

Results

Movement Frequency

We checked whether participants moved at the pacing frequency imposed by the metronome. The magnitude of the deviation of the effective frequency from the metronome frequency was generally small across all conditions (about 0.065 Hz on average), revealing that participants moved at the required frequency. We analyzed data by using a two-way 2 (direction) \times 2 (muscular activation) \times 2 (vision) \times 5 (frequency) ANOVA with repeated measures on all factors. That analysis revealed a significant Muscular Activation \times Frequency interaction effect, $F(4, 24) = 1.71$, $p < .2$, $IE < 0$. A post hoc Newman–Keuls test indicated that both types of muscular activation were significantly different at 3 Hz, $p < .2$ (difference between movement frequencies of both types of muscular activations = 0.046 Hz) and that coactivation of nonhomologous muscle groups displayed the highest deviation value (0.10 Hz).

Percentage of Phase Transitions

A 2 (direction) \times 2 (muscular activation) \times 2 (vision) \times 5 (frequency) ANOVA with repeated measures revealed a statistically significant main effect of direction, $F(1, 6) = 6.02$, $p < .05$, $IE = .05$, muscular activation, $F(1, 6) = 6.29$, $p < .05$, $IE = .02$, frequency, $F(4, 24) = 35.5$, $p < .001$, $IE = .40$, and a significant Direction \times Frequency interaction effect, $F(4, 24) = 7.29$, $p < .001$, $IE = .06$. The number of transitions was larger for nonhomologous than for homologous muscular coupling conditions (61.5% and 38.5%, respectively). A post hoc Newman–Keuls test performed on the significant Direction \times Frequency interaction indicated that tasks requiring nonisodirectional coordination exhibited more transitions than did those requiring isodirectional patterns at 2.5 Hz and 3.0 Hz. Moreover, a post hoc Newman–Keuls decomposition indicated that, for isodirectional patterns, the number of phase transitions increased from 1.0 Hz and 1.5 Hz to 2.5 Hz and 3.0 Hz ($p < .05$). For nonisodirectional patterns, the number of phase transitions increased (a) from 1.0 Hz to 2.0 Hz, 2.5 Hz, and 3.0 Hz, (b) from 1.5 Hz and 2.0 Hz to 2.5 Hz and 3.0 Hz, and (c) from 2.5 Hz to 3.0 Hz (Figure 4).

Time to Transition

We conducted a 2 (direction) \times 2 (muscular activation) \times 2 (vision) \times 5 (frequency) ANOVA with repeated measures on the time-to-transition values obtained for each participant in all experimental conditions. That analysis revealed a sig-

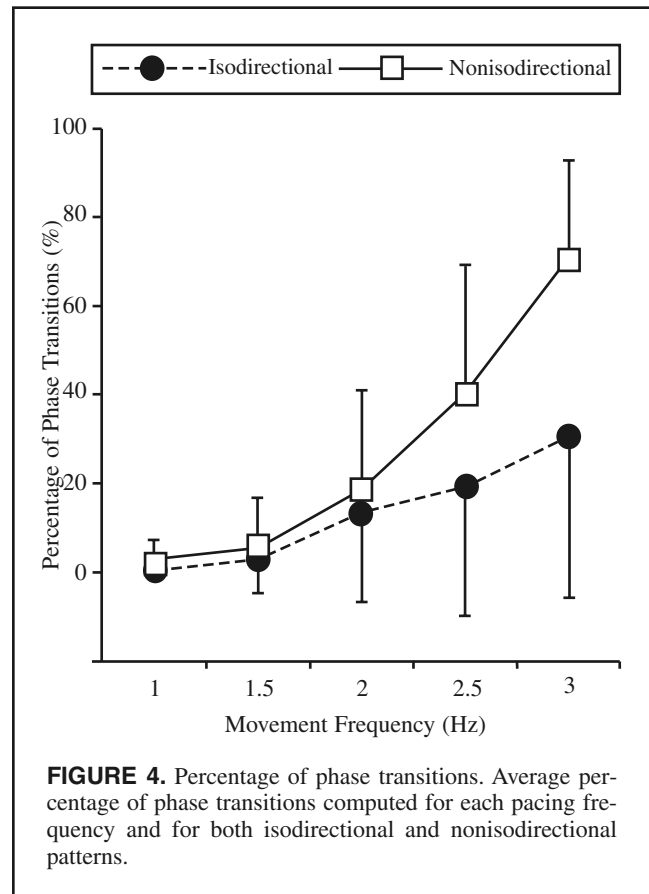
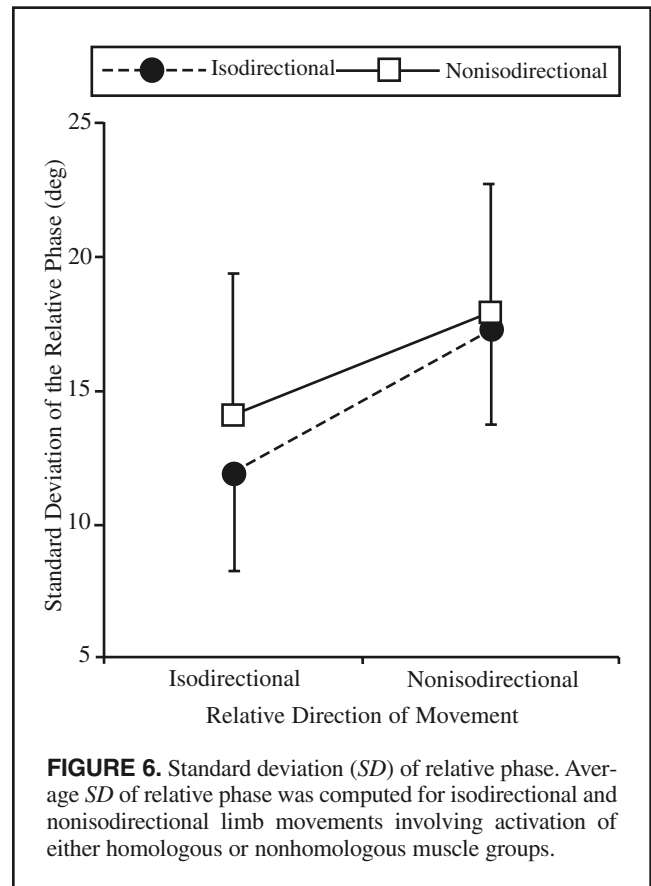
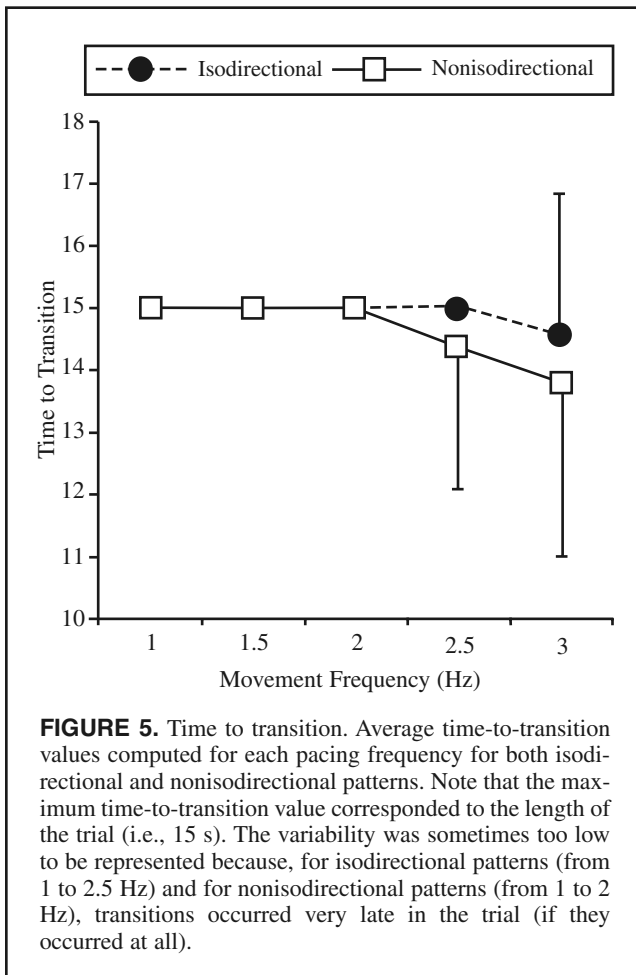


FIGURE 4. Percentage of phase transitions. Average percentage of phase transitions computed for each pacing frequency and for both isodirectional and nonisodirectional patterns.

nificant main effect for frequency, $F(4, 24) = 22.5$, $p < .001$, $IE = .34$, as well as a significant Direction \times Frequency interaction, $F(4, 24) = 2.7$, $p < .05$, $IE = .02$. A Newman–Keuls post hoc analysis of the Direction \times Frequency interaction revealed that the time to transition significantly decreased between 2.0 and 3.0 Hz for the nonisodirectional pattern and was significantly lower for nonisodirectional patterns than for isodirectional ones from 2.5 to 3.0 Hz (Figure 5). As can be seen in Figure 5, for both isodirectional and nonisodirectional patterns, average time to transition was close to 15 s at 1.0, 1.5, and 2.0 Hz. That finding confirms that very few transitions were observed at those frequencies (see Figure 4), which explains the average values and the very low variability. Moreover, when some transition occurred, it started very late in the trial.

SD of Relative Phase

We conducted a 2 (direction) \times 2 (muscular activation) \times 2 (vision) \times 5 (frequency) ANOVA with repeated measures on the average *SD* of relative phase obtained for each participant in each experimental condition. The analysis revealed a significant main effect of direction, $F(1, 6) = 21.64$, $p < .01$, $IE = .23$, muscular activation, $F(1, 6) = 9.87$, $p < .05$, $IE = .02$, vision, $F(1, 6) = 8.62$, $p < .05$, $IE = .01$, and frequency, $F(4, 24) = 39.7$, $p < .001$, $IE = .36$, as well as a significant Direction \times Muscular Activation interaction, $F(1, 6) = 16.66$, $p < .01$, $IE = .01$. Relative phase variability



ty increased with frequency, except from 2.5 Hz to 3.0 Hz. In addition, average values were larger in no-vision conditions than in the vision condition (17° and 15°, respectively). A Newman-Keuls post hoc analysis of the Direction × Muscular Activation interaction revealed that isodirectional patterns were always more stable than nonisodirectional ones, regardless of muscular activation. Moreover, non-homologous patterns were less stable than homologous ones for isodirectional movements but not for nonisodirectional movements (Figure 6).

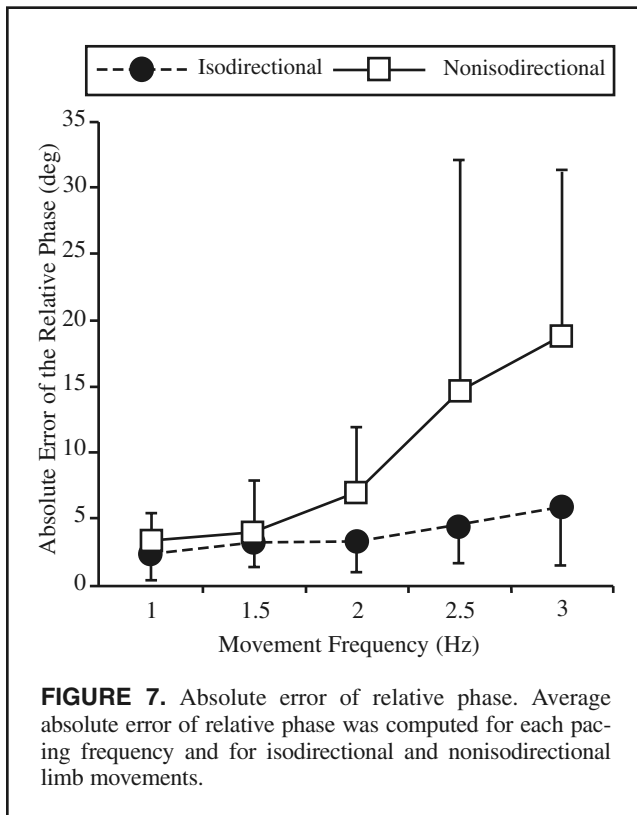
Absolute Error of Relative Phase

We conducted a 2 (direction) × 2 (muscular activation) × 2 (vision) × 5 (frequency) ANOVA with repeated measures on the absolute error of relative phase observed for each participant in the different experimental conditions. The analysis revealed a significant main effect of direction, $F(1, 6) = 10.67, p < .01, IE = .10$, and frequency, $F(4, 24) = 14.42, p < .001, IE = .17$, as well as a significant Direction × Frequency interaction, $F(4, 24) = 4.47, p < .01, IE = .06$. Post hoc Newman-Keuls analysis of the Direction × Frequency interaction indicated that the absolute error of relative phase was larger for nonisodirectional patterns than for isodirectional movements at 2.0, 2.5, and 3.0 Hz. Moreover,

the post hoc decomposition also indicated that for nonisodirectional movements, the absolute error of relative phase increased (a) from 1.5 Hz to 2.0 Hz, 2.5 Hz, and 3.0 Hz, (b) from 2.0 Hz to 2.5 Hz and 3.0 Hz, and (c) from 2.5 Hz to 3.0 Hz ($p < .05$). For the isodirectional patterns, the absolute error showed no significant difference from one frequency to another (Figure 7).

Discussion

We designed the present experiment to investigate the interplay of egocentric and allocentric constraints—that is, (neuro)muscular and directional, respectively—on rhythmic bimanual coordination performed in the sagittal plane of motion. The role played by visual information was also investigated. The results of previous studies have suggested that performing rhythmic coordination between nonhomologous limb components in the sagittal plane of motion favors the dominance of the allocentric constraint (Baldissera et al., 1982; Carson et al., 1995; Kelso et al., 1991; Kelso & Jeka, 1992; Salesse & Temprado, 2005; Salesse et al., 2005). In light of those results, we hypothesized that during bimanual coordination performed in the sagittal plane of motion, the allocentric constraint should play a dominant role in determining pattern stability. The egocentric constraint (coactivation of homologous or nonhomologous muscle groups) would therefore play a subordinate role. We also hypothesized that the effects of the direction-



al constraint could be attributed, at least in part, to visual information. Thus, providing participants with vision of an isodirectional pattern should stabilize bimanual coordination (compared with no-vision conditions). Conversely, vision of a nonisodirectional pattern should have a destabilizing effect.

The analysis of coordination stability revealed that only the frequency of movement had a significant effect on all three indices of stability (i.e., percentage of phase transitions, time to transition, and relative phase variability). That result is not surprising in light of numerous reports of the effect of movement frequency on bimanual coordination stability (for reviews, see Kelso, 1995; Swinnen, 2002).

The analysis of the percentage of phase transitions revealed an effect of both the direction of movement and the coactivation of (non)homologous muscle groups. Observation of the effect intensities revealed that those two factors contributed to the occurrence of transitions in a similar way. With respect to the allocentric constraint, phase transitions predominantly occurred from nonisodirectional to isodirectional patterns. That result is consistent with those observed in studies of hand-foot coordination performed in the same plane of motion (Baldissera et al., 1982; Carson et al., 1995). Transitions were also observed from isodirectional to nonisodirectional patterns at the two highest frequencies, which is consistent with previous findings on intralimb wrist-elbow coordination (Buchanan & Kelso, 1993; Kelso et al., 1991). With respect to the egocentric constraint, phase transitions occurred mainly from simultaneous activation of nonhomologous to simultaneous activation of homologous

muscle groups. However, we also observed that transitions occurred from patterns requiring the coactivation of homologous muscle groups to patterns requiring the coactivation of nonhomologous ones. It is noteworthy that the latter result differs from those repeatedly reported in the literature on bimanual coordination (Kelso, 1984; Monno et al., 2000; Riek et al., 1992). The reason we found a difference from that reported in the existing literature remains uncertain. A speculative interpretation is that, when individuals perform bimanual coordination in the transverse plane of motion, the strength of bimanual coupling results not only from the coactivation of homologous muscle groups but also from the mirror-symmetrical movements with respect to the body midline (for confirming evidence, see Mechsner, Kerzel, Knoblich, & Prinz, 2001; Temprado et al., 2003). Thus, when bimanual coordination is performed in the sagittal plane of motion, the mirror-symmetry effect disappears. The strength of coupling caused by the coactivation of homologous muscle groups is then lower compared with that in the transverse plane. That difference could explain why phase transitions occurred from patterns involving the coactivation of homologous muscle groups to those involving the coactivation of nonhomologous ones.

The analysis performed on the variability of relative phase confirmed that nonisodirectional patterns were more variable than isodirectional ones. Moreover, patterns performed with simultaneous activation of nonhomologous muscle groups were more variable than were those performed with simultaneous activation of homologous muscle groups, except for nonisodirectional movements. Most interesting, the analysis of the effect intensities revealed a stronger influence of direction over activation of muscle groups. Finally, it is noteworthy that movement direction influenced the time to transition, whereas muscle activation did not significantly affect that variable—neither as a main effect nor as part of an interaction. Those results provide us with strong evidence that, in the present experimental context, a dominance of the allocentric over the egocentric constraint was observed on bimanual coordination stability.

Pattern accuracy was also affected by the egocentric and the allocentric constraints. Indeed, at high movement frequencies, execution of bimanual patterns was more accurate for isodirectional than for nonisodirectional movements, as revealed by the evolution of the absolute error of relative phase. Those results are consistent with those reported by Park, Collins, and Turvey (2001), suggesting that in bimanual coordination, spatial (allocentric) constraints influence pattern accuracy. However, our findings do not confirm Park and colleagues' assumption that spatial constraints are exclusively related to pattern accuracy (i.e., phase shift). Indeed, allocentric constraints appeared to influence both pattern stability and accuracy in the present study.

In light of our results, it can be concluded that, as expected, the egocentric (muscular) constraint affected bimanual coordination dynamics (Kelso, 1984; Monno et al., 2000; Riek et al., 1992). Indeed, coordination patterns engaging

simultaneous activation of homologous muscle groups were more stable and exhibited fewer transitions than did those in which nonhomologous muscle groups were coactivated. A striking result of the present study is that the allocentric (directional) constraint was dominant over the egocentric (muscular) constraint on pattern stability. There remains the caveat that, by altering the orientation of the forearm, the relative contributions of both the flexor and the extensor muscles to the rotation of the wrist are changed. Thus, one cannot exclude the possibility that the directional effect could be mediated, at least in part, by subtle changes in the nature of the muscle activation patterns that gave rise to wrist movement in each condition (Carson et al., 2000). Nevertheless, because no difference in pattern stability was found between prone-prone and supine-supine conditions (cf. Temprado et al., 2003), changes in muscle activity patterns seem to have trifling consequences at the coordination level in the present experimental context. Those findings must be considered in light of previous studies on hand-foot (Baldissera et al., 1982; Carson et al., 1995; Salesse & Temprado, 2005; Salesse et al., 2005), arm-leg (Jeka & Kelso, 1995; Kelso & Jeka, 1992), and wrist-elbow coordination (Buchanan & Kelso, 1993; Kelso et al., 1991). In those studies, movements were performed in the sagittal plane of motion, and results showed that the allocentric constraint (i.e., the constraint resulting from the relative direction of moving limbs), rather than the egocentric constraint (i.e., the one caused by muscular activation), was the primary factor determining coordination stability and pattern changes. Not only do the results of our experiment corroborate such observations, they also extend those findings on nonhomologous limbs coordination to bimanual coordination.

Given the noticeable difference between the present results and those observed when the coordination is performed in the transverse plane (e.g., Kelso, 1984; Monno et al., 2000; Riek et al., 1992), the present study does lend credence to the general idea that movement coordination emerges from a coalition of constraints of various origins (Kelso, Fink, DeLaplain, & Carson, 2001; Oullier et al., 2003; Temprado et al., 2003). Indeed, the present results go beyond confirming the existence of a context dependence for the coalition of constraints: They suggest that the relative contribution of egocentric and allocentric constraints to that coalition may vary from one plane of motion to another (see also Serrien et al., 1999; Temprado et al., 2003).

The question remains whether the observed influence of the allocentric constraint is to be sought at the efferent (central commands), the afferent (visual, proprioceptive), or at both levels of movement organization (Swinnen et al., 2003). The results of the present study showed that removing visual feedback slightly destabilized both isodirectional and nonisodirectional movements, regardless of the muscle groups involved in coordination patterns. It is noteworthy that that manipulation did not influence the percentage of phase transitions. Such a result was rather unexpected, considering that in many studies, visual scenes characterized by stimuli moving

in the same direction were perceived more accurately and consistently than were other motion structures (Bingham et al., 2001; Bogaerts et al., 2003; Salesse et al., 2005; Temprado & Laurent, 2004). Thus, it appears that despite the existence of common underlying principles that govern both the perceived motion pattern and the generation of bimanual coordination patterns in the sagittal plane of motion, the motor system apparently did not exploit visual grouping principles to monitor the production of coordination. Hence, in the present task context, our results argue for considering the visual grouping principles to be of minor importance relative to the other (efferent and proprioceptive afferent) sources of information that contribute to bimanual coordination stability. Those results are in line with previous findings obtained in a hand-foot coordination task (Salesse & Temprado, 2005). More important, they do not at all support recent conclusions favoring an exclusive role of perceptual factors in determining bimanual coordination stability (Mechsner, 2004a, 2004b; Mechsner et al., 2001; Mechsner & Knoblich, 2004). However, the hypothesis that kinesthetic afferences may also have a pronounced effect on the control of the nonisodirectional mode of bimanual coordination compared with their effect on the isodirectional mode still needs to be tested for movements performed in the sagittal plane (Swinnen et al., 2003).

Overall, the present results argue in favor of the notion that dissociated processes mediate directional and muscular coding in bimanual coordination performed in the sagittal plane of motion (see Temprado & Swinnen, 2005, for a converging conclusion on learning). The exact basis of muscular and directional coding remains uncertain, however (for a review, see Debaere et al., 2001). Results of recent neurophysiological studies favor an efferent locus of spatial constraints in the production of unimanual and bimanual movements (Kakei, Hoffman, & Strick, 1999, 2001, 2003; Paz & Vaadia, 2004; Steinberg et al., 2002) as well as in hand-foot coordination (Baldissera, Borroni, Cavallari, & Cerri, 2002; Borroni, Cerri, & Baldissera, 2004). For instance, Steinberg et al. have shown that specific cells in the motor cortex accurately predict the direction of movement for both unimanual and bimanual movements, even when the two arms move simultaneously in different directions. Moreover, other investigators have reported that groups of cells in the primary motor cortex and the ventral premotor cortex code information about the direction of movements in space quite independently of the activity of groups of cells coding information relative to muscular activity (Kakei et al.; for consistent results on learning, also see Paz & Vaadia, 2004).

In conclusion, the results of the present study shed light on how egocentric (muscular) and allocentric (directional) constraints interplay for bimanual coordination in the sagittal plane of motion. In such a context, they indicate that allocentric constraints were dominant over egocentric ones. The directional dominance markedly differs from the overwhelming role of (neuro)muscular constraints widely reported in the transverse plane of motion. Thus, not only do our results argue for considering the emergence of coor-

dination patterns to be the result of a coalition of multiple constraints, they also strongly suggest that the plane of motion is a key mediator of the coalition of egocentric and allocentric constraints on bimanual coordination. It has been recently suggested that the spatial orientation between limb movements may act as a (symmetry-breaking) parameter that allows other constraints on bimanual coordination to emerge as dominant factors in modulating coordinative stability (see Fuchs & Jirsa, 2000; Lee, Almeida, & Chua, 2002). Our results suggest that the plane of motion in which coordination is executed has a comparable effect. Further studies are necessary, however, to explore whether (and how) the different planes of motion possibly change the coordinate frame that mediates the underlying processes involved in directional and muscular coding of limb movements during bimanual coordination (see Temprado et al., 2003, for early suggestions on that topic).

NOTES

1. In the present study, we defined transverse and sagittal planes of motion with respect to the terminology proposed by Serrien et al. (1999). *Sagittal plane* therefore refers to movements performed in the anteroposterior plane of motion, whereas *transverse plane* refers to movements in the mediolateral plane.

2. In a similar flexion–extension bimanual coordination task performed in the sagittal plane of motion with the same experimental set-up, Temprado et al. (2003) reported no difference in coordination stability between prone–prone and supine–supine forearm positions.

3. The coefficient of determination ω^2 is the proportion of variance in the dependent variable accounted for by the independent variable.

$$\omega^2 = \frac{SS_{\text{Between-groups}} - (k-1) * MS_{\text{Within-groups}}}{SS_{\text{Total}} + MS_{\text{Within-groups}}},$$

where *SS* is sum of squares, *MS* is mean square, and *k* is the number of groups formed by categories of the independent variable. Omega-square (ω^2) normally varies from 0 to 1, but may have negative values when the *F* ratio is near or less than 1. Cohen (1969) calls ω^2 *large* when it is over .15, *medium* when it ranges from .06 to .15, and other values *small*.

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