Published in final edited form as:

J Mot Behav. 2006 September ; 38(5): 383–404.

Effects of Movement Frequency and Joint Kinetics on the Joint Coordination Underlying Bimanual Circle Drawing

Ya-weng Tseng and John P. Scholz

Department of Physical Therapy University of Delaware, Newark

Martin Valere

Institut für Neuroinformatik Ruhr-Universität-Bochum, Germany

Abstract

Ten healthy participants performed bimanual symmetric and asymmetric circle drawing at 4 frequencies. The authors partitioned the variance of the joint configuration across repetitions into 1 component representing equivalent joint configurations with respect to achieving stability of the mean hand path (i.e., goal-equivalent variance, *GEV*) and 1 component leading to a variable hand path (non-goal-equivalent variance, *NGEV*) across cycles. Higher frequencies led to increased *NGEV* related to control of the nondominant hand and to the relative position and orientation between the hands during asymmetric drawing. The results were related to differences in muscle and interaction moments between the arms, and they suggest a possible relationship between the ability to use intersegmental forces and the stability of interlimb synergy.

Keywords

bimanual coordination; kinetics; motor control; multi-segment movement

The successful performance of bimanual activities requires the coordination of motor elements within as well as across the arms. Motor elements may, for example, be joints, muscles, and motor units, depending on one's level of analysis. The number of motor elements is typically greater than the number of task-related variables that describe what is essential for the task, such as the hand's position in a reaching task or the body's center of mass position in a postural task. Coordination of the motor elements is generally considered to involve their combination into fewer units of action, that is, to the formation of functional synergies (Latash, Scholz, Danion, & Schöner, 2002). For performance of unimanual circle drawing, the muscles and, subsequently, joints of each arm are presumably organized into a functional synergy that controls the hand's movement. For bimanual circle drawing, a higher level synergy that unites the motor elements of both arms is presumably also required. For drawing performance to be successful and consistent, the joint synergies must act so that the values of task variables that are most relevant to successful performance, such as the movement paths of the individual hands and the relative motion of the two hands (Carson, Thomas, Summers, Walters, & Semjen, 1997; Semjen, Summers, & Cattaert, 1995; Swinnen, Jardin, & Meulenbroek, 1996; Swinnen et al., 1997; Tseng & Scholz, 2005), are stabilized (Schöner, 1995).

Functional synergies have historically been defined in terms of the average relationship between changes of the elemental variables across time or some other parameter change (Desmurget et al., 1995; Z. M. Li, Latash, & Zatsiorsky, 1998; Macpherson, Rushmer, &

Dunbar, 1986; Pelz, Hayhoe, & Loeber, 2001; Santello & Soechting, 2000). At the extreme, that definition may suggest that the joints or muscles are made completely dependent such that the effector space is essentially nonredundant for the task (Medendorp, Crawford, Henriques, Van Gisbergen, & Gielen, 2000). In more recent accounts, however, the importance of flexibility in synergy formation has been emphasized (Gelfand & Latash, 1998; Latash et al., 2002). According to such accounts, the control system actually uses many possible solutions to combining (i.e., coordinating) the motor elements; those solutions are equivalent in terms of stabilizing the values of important task-relevant variables (Schöner, 1995). For example, consider holding one's finger on a doorbell while wiggling the joints of the arm around in many ways that do not change the fingertip's position. All such joint combinations are equivalent, or represent equivalent solutions to joint coordination, with respect to the fingertip's position. Such flexibility underlies a variety of motor phenomena, such as motor equivalence in response to perturbations (Abbs, Gracco, & Blair, 1984; Hogan, 1985; Kelso, 1984), error compensation for unexpected fluctuations of the values of the motor elements (Latash, Scholz, Danion, & Schöner, 2001; Scholz, Danion, Latash, & Schöner, 2002), and the ability to perform secondary tasks without adversely affecting primary task performance (Krishnamoorthy, Yang, & Scholz, 2005). In the current study, we explored whether motor redundancy is exploited in the synergy formation underlying a bimanual circle-drawing task that we made increasingly challenging by increasing movement frequency (e.g., Byblow, Lewis, Stinear, Austin, & Lynch, 2000; Carson et al., 1997; Cattaert, Semjen, & Summers, 1999; Kelso, 1984; Scholz & Kelso, 1989; Scholz, Kelso, & Schöner, 1987; Semjen et al., 1995; Stucchi & Viviani, 1993; Wuyts, Summers, Carson, Byblow, & Semjen, 1996).

In most studies of bimanual circle drawing, the stability of patterns of bimanual coordination related to the relative phasing of the two hands' motion, or similar measures, such as the relative tangential angle between their movements, have been examined (e.g., Byblow et al., 2000; Carson et al., 1997; Cattaert et al., 1999; Kelso, 1984; Scholz & Kelso, 1989; Scholz et al., 1987; Semjen et al., 1995; Stucchi & Viviani, 1993; Wuyts et al., 1996). In many cases, the size of the object being drawn has rendered the task relatively nonredundant in terms of joint motions, although the action of the individual joints has not typically received detailed consideration. Investigators have used relative phase measures to explore the qualitative dynamics of interlimb coordination, with an eye toward understanding the stability of interlimb coordination patterns under different task conditions. Although the information provided by such analyses is quite valuable, an understanding of how the many degrees of freedom (*dfs*) of the arm are coordinated to achieve stable individual and relative hand control when the system is redundant is lacking. The motor system obviously does not use all possible combinations of the redundant *dfs* to control the hand's movement, but a growing body of literature suggests that the nervous system typically takes advantage of a range of equivalent joint combinations to control various upper-extremity tasks (Domkin, Laczko, Jaric, Johansson, & Latash, 2002; Latash et al., 2001; Tseng, Scholz, Schöner, & Hotchkiss, 2003; Tseng & Scholz, 2005; Yang & Scholz, 2005). That is, output variability of elemental variables does not reflect primarily noise or error.

In the current study, we used the uncontrolled manifold (UCM) approach (Scholz & Schöner, 1999) to address the flexibility of functional synergies used in bimanual circle drawing. The advantage of that approach (see Materials and Method) is that it provides information about the coordination among many motor elements simultaneously, not only pairs of elements, and not in isolation but in relation to the control of task-relevant variables. Thus, the analysis is more objective than is an approach such as principal component analysis, which is subjective and provides information only about the average sharing pattern among the motor elements. We used the UCM analysis to examine the coordination of joint motions of the individual arms with respect to control of individual hand paths as well as the coordination of the joint motions of both arms in relation to control of the relative movement of the two hands, as indexed by

the vector difference between the two hands' positions at any point in time. That technique contrasts with the method used in previous examinations of the relative phasing, or timing, between the hands' motions in the study of bimanual coordination.

We also sought in this study to determine whether there are differences between the arms in the use of flexible patterns of joint coordination and whether those differences are related to the control of intersegmental dynamics. Passive interaction moments arise as a result of the mutual influence between arm segments during the execution of multijoint movements (Hollerbach & Flash, 1982). The apparent inability to adequately predict or deal with interaction moments, or both, has been associated with movement deficits of patients with sensory loss (Ghez, Gordon, & Ghilardi, 1995; Sainburg, Ghilardi, Poizner, & Ghez, 1995), patients following a stroke (Beer, Dewald, & Rymer, 2000), and patients with cerebellar disorders (Bastian, Martin, Keating, & Thach, 1996). Moreover, differences in the ability of the dominant and the nondominant arms to deal with interaction moments have been shown during performance of a two-joint reaching task in right-hand-dominant individuals (Bagesteiro & Sainburg, 2002; Sainburg & Kalakanis, 2000). Sainburg and his colleagues found that motions of the nondominant, left elbow resulted primarily from the elbow muscle moment, whereas elbow motions in the dominant, right arm resulted from a combination of elbow muscle moment and the interaction moment resulting from the shoulder's action. That is, the motor system presumably achieved control of the dominant elbow by anticipating the influence of intersegmental dynamics and taking advantage of those dynamics. They also reported that deviation of the nondominant hand's path from the desired direction was dependent on the extent to which the control system accounted for the intersegmental dynamics. However, the same result was not found for the dominant arm (Sainburg & Kalakanis). Thus, they suggested that those results imply different neural mechanisms for control of the dominant and nondominant limbs. The results could, however, also reflect more limited ability to use sensory information from the nondominant limb to help structure the control signal to that arm. In addition, in most of that work, investigators have examined task performance by using a set of nonredundant joints, making it difficult to assess the role of dynamics in typically redundant tasks.

Dounskaia, Swinnen, Walter, Spaepen, and Verschueren (1998) reported how rhythmical elbow and wrist movement patterns change as a result of increasing intersegmental interactions. When individuals were required to move at a faster rate, coordination of the two joints deteriorated because of an increasing negative effect of the interaction moment, which required them to use additional muscle activity to compensate. Ultimately, that resulted in a movement pattern in which (a) the distal joint (i.e., wrist) showed little electromyographic activities and (b) its motion was predominantly governed by interaction effects from the proximal joint (i.e., elbow). It is reasonable to predict on the basis of Dounskaia and her colleagues' results that such effects should have a greater influence on control of the nondominant hand than on control of the dominant hand for right-handed participants when oscillating at a higher pace. For the bimanual circle-drawing task examined in the current study, if such an effect exists, then it should also affect the ability to produce stable relative motion between the two hands. Alternatively, if a synergy uniting the joints of the two arms in that bimanual task is somewhat independent of the synergies controlling individual hand movement, then the effect of interaction moment on control of the nondominant hand would be predicted to be less detrimental to the relative motion of the two hands than to that hand's movement.

In this study, we also examined the effect of additional visual attention on the coordination of the hands. We hypothesized that when the task required tracing a visible circular template, compared with drawing a remembered path, participants would require greater focus on maintaining stable individual hand paths in order to accurately trace the template, leading to poorer control of the relative position and orientation of the two hands. We expected to see

higher joint variance, which would lead to variations of the vector difference between the hands when participants traced the physical template in comparison with those when participants traced the remembered circular path.

Materials and Method

Participants

Ten healthy young participants (3 women and 7 men, mean age = 23 ± 3.97 years) were recruited from the university campus. The Human Subject Review Board at the University of Delaware approved the experimental protocol and the consent form for this study. All participants were self-identified as right-handers, and we confirmed their hand-dominance by using the 10-item Edinburgh Handedness Inventory (Oldfield, 1971). Therefore, we examined only right-hand-dominant individuals. All participants were naive about our purpose in the study.

Motion Analysis

We used a six-camera infrared motion measurement system (VICON, Oxford Metrics, Oxford, UK) to record planar motion of two arms when participants performed circular drawing movements. The cameras were mounted on the ceiling in a semicircle, anterior and lateral to the participant. We calibrated the cameras before each data collection and used them to capture arm movements at 120 Hz. After calibration, the positive global *X*-coordinate represented the rightward direction (mediolateral), and the positive global *Y*-coordinate represented the forward direction (anteroposterior). The positive *Z*-coordinate pointed upward. We attached individual reflective markers with adhesive-backed Velcro to the skin overlying the following bony landmarks: (a) sternal notch, (b) just inferior to the lateral edge of acromion process (shoulder), (c) lateral epicondyle of the humerus (elbow), (d) radial styloid process (wrist), and (e) distal end of the second metacarpal bone.

Experimental Setup

Participants sat on an adjustable-height, high-back chair at a rectangular table (122 cm $\times$ 91 cm) with a flat surface (see Figure 1A). We adjusted chair height so that the upper arm and forearm were horizontal and parallel to the tabletop when participants held the drawing tool by using a power grip (thumb pointing toward the midline). We used the table to support the drawing implement, an emptied roll-on deodorant bottle, and we drew a template of the circle to be traced with liquid chalk on the tabletop. The chalk dried in about 1 min and stayed on during the entire experiment. The participants traced the appropriate physical template with the drawing implement. We attached each participant's hand to the side of the bottle with Velcro to prevent movements between the hand and the bottle. Motions of the arm in the vertical dimension (*Z*-coordinate) were minimal because the drawing implement had to remain on the tabletop in this drawing task. We monitored the vertical excursion of the elbow marker during the experiment to check that it was kept to a minimum. Vertical motion of the elbow averaged 2.21 ± 0.17 cm across all participants and conditions. In addition, we placed the participants' upper chest snugly against the edge of the table to prevent trunk motion. The snug position, along with a wide strap that encompassed the participant's upper trunk and the chair back, prevented trunk motion. In addition, we reminded participants to move only the arm and scapula when performing the drawing task. One experimenter also observed the participants to ensure that the trunk was stable during the experiment.

We centered the placement of the drawing template at the participant's shoulder (right or left, respectively) and set the bottom of the template at 50% of the upper-arm length of each participant from the edge of the table. We determined the size of the template on the basis of the participant's arm length, measured from the acromion to the second proximal

interphalangeal joint. The diameter of the template was set at 40% of the measured arm length. Thus, template size was scaled to each participant's anthropometry. The actual diameter of the template ranged from 25 to 30 cm (median = 28.75 cm). We set the size of the template to ensure that motions occurred in all four joints (scapula, shoulder, elbow, and wrist) of an arm. In the starting position, in which the drawing implement was positioned at the lower bottom of the circle (6 o'clock position), we measured joint angles with a goniometer before each trial to ensure a constant initial arm configuration. We used a computer-generated metronome pulse to pace the drawing movements.

Procedure

We instructed participants to produce smooth and continuous circle-drawing movements while following a metronome beat. There were four 8-s frequency levels: 1.0, 1.5, 2.0, and 2.5 Hz. Therefore, the duration of each trial was 32 s. The experiment involved performance of five randomized trials per each of two drawing patterns, performed with and without a circular-drawing template. The two drawing patterns were as follows: (a) Symmetric, that is, simultaneous inward movement of both hands beginning from the starting position (see Figure 1B). Participants performed the inward movement direction by moving the dominant hand clockwise and the nondominant hand counterclockwise. (b) Asymmetric, that is, simultaneous rightward movement of both hands (i.e., performed in the counterclockwise direction; see Figure 1C). Participants performed the with-template condition first with both patterns, and we then instructed them to memorize the location and size of the template before we removed the chalk-drawn template from the tabletop. Another five trials of each symmetric and asymmetric movement pattern were then performed in the no-template condition, but we asked participants to follow the memorized traces. We placed a dot midway between the two templates as a gaze point for participants in all conditions. We instructed them to keep their eyes focused on that point while performing the task.

Data Analysis

Reconstruction of marker position—We digitized the marker data online and reconstructed the three-dimensional (3D) coordinates from the two-dimensional (2D) coordinates of the six cameras offline by using the VICON software. Reconstructed marker coordinates were filtered with a bidirectional, second-order Butterworth low-pass filter in MATLAB (The MathWorks, Natick, MA). The cutoff frequency was 5 Hz.

Calculation of joint angles—We calculated the planar 2D angle between adjacent limb segments by using a link-segment model (Figure 2A). For example, the vector connecting the shoulder and the sternum markers defined the orientation of the clavicle (V1), whereas the vector connecting the shoulder and elbow markers (V2) defined the orientation of the upper arm segment. The angle between those two vectors, after normalization, defined the shoulder angle (Θ_2), for example,

$$\Theta_2 = \text{Arc cosine} \left(\frac{V_1}{|V_1|} \cdot \frac{V_2}{|V_2|} \right). \quad (1)$$

We computed four angles in each arm: scapular (clavicular) abduction–adduction, shoulder horizontal abduction–adduction, elbow flexion–extension, and wrist flexion–extension. We determined segment lengths by computing the vector length between each adjacent pair of joint markers. That information was used for the geometric model (see UCM analysis).

UCM analysis—We used the UCM method to quantify the extent to which participants used flexible, equivalent combinations of joint motions to control two task variables important to successful bimanual circle drawing: (a) the movement path of each hand and (b) the vector difference between the hands. According to the UCM hypothesis, the motor control system

restricts combinations of *dfs* that lead to undesired fluctuations in the value of an important task variable, whereas it allows different combinations of *dfs* that lead to an equivalent, “desired” value of the same task variable, leading to the observation of flexible solutions to combining the motor elements. The extent of the flexibility depends on whether other task constraints are present or on the performance of secondary tasks that limit the combinations of motor elements allowed. To discover and interpret the structure of variance (and hence of stability) in the space of motor elements (e.g., joint motions), one must link task variables to directions in the space of the motor elements. That can be achieved, in many cases, through geometric models of the limb that indicate how variations of the joint combinations along particular directions in the space of the joints affect, for example, the hand's position. Scholz and Schöner (1999) developed a technical procedure, the method of the “uncontrolled manifold,” with which one can test hypotheses about relevant task variables by transforming them into hypotheses about the structure of variance in joint space.

To illustrate the UCM concept, we provide In Figure 2B a schematic example of three single-axis joint angles (shoulder, elbow, and wrist) used to control the planar position of the hand. Given motor redundancy, an individual could adopt many different combinations of the three joint angles to achieve a particular planar hand position. For example, J_1 , J_2 , and J_3 are three of many equivalent combinations of the three joint angles that yield hand position H_1 . All such combinations can be represented as a subspace, or manifold, in the space of the three joint angles—in this example, a line (solid line, Figure 2C). Likewise, joint combinations J_4 and J_5 are two of a large number of joint-angle combinations that are equivalent with respect to producing hand position H_2 (dotted line, Figure 2C). If J_1 , J_2 , and J_3 are actually realized over repetitions of the task, then the variance computed across joint configurations is considered goal equivalent with respect to achieving hand position H_1 , whereas the variance computed across joint configurations J_4 and J_5 , and others lying off of the H_1 manifold (solid line, Figure 2C) is non-goal-equivalent variant (*NGEV*) with respect to control of H_1 . A similar argument can be made about the variance of joint combinations J_4 and J_5 , with respect to hand position H_2 . For example, consider that H_1 represents the hand's position achieved at some percentage of the movement cycle when a circle is traced with a three-*df* arm. The participant begins the trial of circle drawing at 6 o'clock and performs multiple cycles (defined from one 6-o'clock position to the next 6-o'clock position) per trial. If the amplitude and timing of drawing is well controlled, then we can expect that at a given percentage of cycle completion the hand will be at approximately the same position, for example, H_1 . If the motor system accomplishes that by invoking additional task constraints or cost functions to achieve a unique solution to joint coordination across cycles (e.g., J_2), then there would be no goal-equivalent variance (*GEV*), whereas *NGEV* would be present to the extent that the hand does not exactly achieve H_1 on each cycle at the reference percentage of the cycle. Alternatively, if the motor system achieves H_1 successfully at the same percentage across cycles by using a variety of equivalent joint combinations, for example, J_1 , J_2 , and J_3 , then one can expect *GEV* to be greater than *NGEV*, the size of the latter component depending on how well the system actually controls the hand motion to achieve H_1 at that percentage of the cycle. One partitions joint configuration variance into *GEV* and *NGEV* by using the UCM method, and partitioning is performed at every 1% of the movement cycle under the assumption that the movement is accomplished by a specific timing of shifts of the system's states (Feldman, 1986).

According to the UCM hypothesis, then, *GEV* is expected to be larger than *NGEV* for the control of important task variables. If the *NGEV* component were found to be quite large compared with the *GEV* component when they are evaluated with respect to a particular variable, despite successful task performance, then control of the hypothesized task variable would not be considered crucial for this task but may be important for another task. For example, control of the spatial position of the pointer tip is important in a reach-to-point task (Domkin et al., 2002; Tseng, Scholz, & Schöner, 2002; Tseng et al., 2003), but control of the

exact spatial position of the tip of a gun is apparently not crucial for shooting at targets (Scholz, Schöner, & Latash, 2000). The latter observation was associated with a larger *NGEV* than *GEV*, or both components of variance were almost equal.

Implementing the UCM approach involves the following steps:

1. Develop a geometric model linking the value of a task variable of interest, for example, the *X*- and *Y*-coordinates of the hand position, to the value of relevant joint angles:

$$\mathbf{x} = l_1 \times \cos(\theta_1) + l_2 \times \cos(\theta_1 + \theta_2) + l_3 \times \cos(\theta_1 + \theta_2 + \theta_3) + l_4 \times \cos(\theta_1 + \theta_2 + \theta_3 + \theta_4), \quad (2)$$

$$\mathbf{y} = l_1 \times \sin(\theta_1) + l_2 \times \sin(\theta_1 + \theta_2) + l_3 \times \sin(\theta_1 + \theta_2 + \theta_3) + l_4 \times \sin(\theta_1 + \theta_2 + \theta_3 + \theta_4), \quad (3)$$

where l_1 = length of the clavicle, l_2 = length of the upperarm segment, l_3 = length of the forearm segment, and l_4 = length of the hand (see Figure 2A for an illustration of θ s).

2. Compute a linear estimate of the subspace of all combinations of joint angles in the angle space that leads to an identical value of the desired task variable, at each percentage of the movement. The mean value of the joint configuration (θ_0) across trials is used as an estimate of the desired value of the task variable. Given the nature of the current task, tracing a displayed template, one could assume that the desired value of the hand position corresponds to a position on the template at a particular point in time. Even if the movement timing were perfect, however, determining a joint combination that corresponds to a given hand position on the circle is an ill-posed problem because of the inherent redundancy. In the current analysis, we therefore used the mean position of the hand to estimate the desired hand position. The subspace defined as an uncontrolled manifold (UCM) is obtained as the null-space of the Jacobian matrix relating changes in the joint-angle configuration to changes in the task variable (for details, see Scholz et al., 2000).

$$\mathbf{r} - \mathbf{r}_0 = \mathbf{J}(\theta_0) (\theta - \theta_0), \quad (4)$$

where $\mathbf{r}$ and $\mathbf{r}_0$ represent the values of the task variables that correspond to the current and mean configurations of the joint angles, respectively. $\mathbf{J}(\theta_0)$ is the Jacobian, or the matrix of partial derivatives of the task variable with respect to the mean joint-angle configuration. θ is the actual value of the joint configuration for a given drawing cycle. The null-space is spanned by basis vectors, $\mathbf{e}_i$, solving

$$0 = \mathbf{J}(\theta_0) \mathbf{e}_i. \quad (5)$$

There are $n - d$ basis vectors spanning the null-space (n joints minus d task-variable coordinates; e.g., $4 - 1 = 3$, when considering four angles controlling a one-dimensional position of the hand). One uses MATLAB to numerically compute the $\mathbf{e}_i$ s at each time slice.

3. At each point in the movement cycle, we rendered the current vector of joint angles observed during performance of the task mean-free by subtracting the vector of the mean joint configuration ($\theta - \theta_0$), and we projected it onto each dimension of the null-space or UCM; that is,

$$\theta_{\perp} = \sum_{i=1}^{n-d} \left[\mathbf{e}_i^T \cdot (\theta - \theta_0) \right] \mathbf{e}_i, \quad (6)$$

as well as orthogonal to the UCM, that is,

$$\theta_{\perp} = (\theta - \theta^0) - \theta_{\parallel}. \quad (7)$$

4. One computes the variance of the projections parallel and orthogonal to the UCM across cycles at each percentage of the movement cycle and then normalizes the result to the appropriate *dfs* to yield the estimates of *GEV* (Equation 8) and *NGEV* (Equation 9), respectively.

$$\sigma_{\parallel}^2 = \sum \theta^2 / [(n - d)N_{\text{cycles}}], \quad (8)$$

$$\sigma_{\perp}^2 = \sum \theta^2 / (dN_{\text{cycles}}), \quad (9)$$

where the summation is over cycles for a given percentage of the cycle, and $\theta_{\parallel}^2$ and $\theta_{\perp}^2$ are the squared length of the $\theta_{\parallel}$ and $\theta_{\perp}$ vectors lying within and orthogonal to the linearized UCM, respectively.

We chose the cycles used in the actual analysis on the basis of both timing and spatial performance. We eliminated from further analysis cycles that did not have consistent timing (mean cycle period ± 1.75 standard deviations [*SD*]) compared with other cycles or did not start the cycle at a consistent position (mean start location ± 1.75 *SD*). On average, we used approximately 30–50 cycles for the analysis, depending on the movement frequency.

Although one could, in principle, apply the UCM analysis to the examination of joint coordination related to interlimb timing by treating relative phase as a task variable, solving analytically for the Jacobian of a function containing the sine and cosine functions of eight joints (as in the present experiment) has proved intractable.

Independent Variables

The independent variables in this study were the arm used to draw (nondominant or dominant), the movement pattern (symmetric or asymmetric), template condition (with or without), and movement frequency (1.0, 1.5, 2.0, and 2.5 Hz).

Dependent Variables

Components of joint configuration variance—The major dependent variables in this study were the two components of joint configuration variance, namely, *GEV* and *NGEV*. We separately evaluated hypotheses about controlling the individual hand's 2D position and the vector difference between the two hands. For the latter analysis, we subtracted the 2D coordinates of the right hand's position, expressed through the geometric model as sine–cosine functions of joint angles and segment lengths of the right arm (see Equations 2 and 3), from a similar function of the 2D coordinates of the left hand's position. The resulting vector difference between the hands carries a length and direction in external space. We computed the averaged components of joint configuration variance over the entire cycle for presentation and statistical analyses.

Kinematic variables—We examined the following variables to provide a measure of movement performance of the drawing tasks.

1. Cycle period: We first determined cycle period by using an event-picking algorithm written in MATLAB. The algorithm picked the value of minimal positions of the trajectory in the forward–backward (FB) dimension. The duration between two successive crossings of minima in the FB dimension defined the start and stop of a cycle. We then compared the actual cycle period with the required period corresponding to each frequency level, for example, 500 ms at

2.0 Hz (i.e., average performed period minus required period). The value of the deviation would be negative if participants moved faster than the required period, whereas the value would be positive if they moved slower.

2. Mean circle diameter: The averaged diameter in the mediolateral (ML) and FB dimensions determines the size of the circle. We used a peak-picking algorithm written in MATLAB to pick the value of maximal and minimal positions of the trajectory in the ML dimension. Then, we calculated the difference between the maximum and the minimum of the ML dimension to yield the circle diameter in the ML dimension. We applied the same calculation to the FB trajectory to yield the diameter in the FB dimension. The averaged value of ML and FB diameters was an approximation of the circle diameter during each cycle. Nonetheless, some distortions in the shape of the object drawn were expected, and that calculation may not yield the exact measure of its size. We computed the mean circle size across all cycles and then across participants.

3. Circularity: We characterized the shape of the trajectory produced in each movement cycle, following Walters and Carson (1997). The core of that technique is to derive the best-fitting ellipse for an enclosed contour such as the circle-drawing trajectory. The ratio of the lengths of the major and minor axes of the best-fitting ellipse provides an index of circularity. A circularity index of 1 indicates a perfect circle, whereas a circularity index of 0 indicates a straight line.

4. Variability of individual hand paths: We computed the mean and *SD* of each hand's path and used the coefficient of variation ($CV = M/SD \times 100$) to provide a measure of relative consistency of the hand path, given the significant change of circle size over frequency scaling.

5. Variability of the vector difference between the two hands: A vector that carries a length and direction component represents the relative position and orientation between two hands. We represented the length of that vector by calculating the distance between two hands. The *SD* of that relative distance across cycles was then calculated. The cosine of that vector with respect to the horizontal axis determined vector orientation, and we also used the *SD* to assess variability.

Kinetic analysis—We determined the moment acting at each joint of the arm in the horizontal plane by using a dynamic link-segment model (see Figure 2A for the arrangement of joint angles). Using anthropometric data (Hanavan, 1964; Winter, 1979), we estimated segmental masses, segmental center of mass locations, and moments of inertia about the vertical axes passing through the joint centers. The dynamics equations for the four-joint manipulator were derived from the Lagrange's equation within the screw theory framework (Murray, Li, & Sastry, 1994). The screw theory rests on the fact that any rigid body can be moved from any one position to any other by a movement consisting of rotation about a straight line followed by a translation parallel to that line. That movement is called a *screw motion*. An infinitesimal screw motion is called a *twist* and provides a description of the instantaneous velocity of a rigid body. Two main advantages of the screw theory are, first, it does not suffer from singularities because of the use of local coordinates and, second, it provides a geometric description of a rigid body motion. Using the product of exponential formulas to describe the geometry of the arm, we computed the orientation and position of the coordinate system attached to the center of mass of each arm segment. We then obtained the velocity of each segment with the respective Jacobian matrix. We computed the energy of the arm by summing the kinetic and potential energy for each segment, which then allowed the application of the Lagrange's equation. We computed the dynamics equations analytically by using Mathematica

Version 5.0 (Wolfram Research, Inc., Champaign, IL). The general formulation of equations of motion can be represented as

$$M(\theta) * \ddot{\theta} + H(\theta, \dot{\theta}) = \tau_{\text{muscle}} \quad (10)$$

where $H(\theta, \dot{\theta})$ is a combination of Coriolis and centrifugal forces acting at each joint that depends on the motion and position of the other joints. The generalized muscle moment (MM), τ_{muscle} , includes active muscle activity and passive forces arising from the viscoelastic properties of muscles, tendons, ligaments, and periarticular soft tissues. There is no gravitational moment because movement is constrained in a horizontal plane. $M(\theta)$ is a 4×4 , configuration-dependent inertial matrix, $\ddot{\theta}$, $\dot{\theta}$, and θ are the vectors of joint acceleration, velocity, and angle, respectively. The inertial matrix $M(\theta)$ has diagonal entries corresponding to the inertia of a given segment of interest and off-diagonal entries capturing the effect on each joint based on the acceleration of the other joints. By separating out the two components of the inertial matrix, $M_d(\theta)$ and $M_{nd}(\theta)$, one can write Equation (10) as

$$M_d(\theta) * \ddot{\theta} = -M_{nd}(\theta) * \ddot{\theta} - H(\theta, \dot{\theta}) + \tau_{\text{muscle}} \quad (11)$$

One can further represent Equation 11 as the following by grouping the appropriate terms for interaction moments:

$$NM = IM + MM \quad (12)$$

NM is proportional to joint acceleration and is directly responsible for motion of that joint. IM is the interaction moment; it depends on mutual interactions with the other joints. MM represents the generalized muscle moment. See the Appendix for each component of $M(\theta)$ and $H(\theta, \dot{\theta})$.

After qualitatively examining the continuous moment profile to identify the general organization of moment components of each joint, we conducted analyses of the sign of the moments and the moment impulse. Intervals during which IM had the same or an opposite sign compared with NM were considered to make a positive or a negative contribution, respectively, to NM . Positive contribution was considered as assisting NM , whereas negative contribution was considered as resisting NM . We determined the percentage of positive and negative contribution intervals relative to total cycle period. We computed the positive or negative moment impulse (moment * time) during intervals in which the IM component acted in the same or an opposite direction compared with NM . Muscle moment impulse was likewise computed as a contribution to net moment. We summed all positive and negative impulses for each moment component within each cycle to yield a measure of total moment impulse.

Statistical Analyses

We performed repeated measures analyses of variance (ANOVAs) to evaluate differences in the relative amount of the two components of joint configuration variance as well as other kinematic variables by using SPSS Version 13.0 software (SPSS, Inc., Chicago, IL). For control of the individual hands, we performed a 2 (arm) $\times$ 2 (template) $\times$ 2 (movement pattern) $\times$ 4 (frequency) within-participants design on individual variance components (GEV or $NGEV$) as well as on other kinematic and kinetic variables. To test control of the vector difference between two hands, we used a 2 (template) $\times$ 2 (movement pattern) $\times$ 4 (frequency) within-participants design. We performed post hoc analyses for comparisons on the basis of our hypotheses, using the m-matrix structure in SPSS.

We were also interested in how variations of the interaction moment (evaluated as the moment impulse) would account for the variability of each hand's path. We performed linear regression

analysis between the variability of the individual hand path and the variability of the interaction moment impulse by using SPSS. Our underlying assumption was that to the extent that the control system did not fully account for or compensate for variations of the interaction moment, that would lead to variations of the hand path (e.g., Sainburg & Kalakanis, 2000).

Results

Circle and Hand Kinematics

The results of cycle period deviation, circle size, and circularity are summarized in Table 1. Main effects for arm, pattern, template, and frequency are shown, and the statistical significance is indicated accordingly. An illustration of drawing performance is provided in Figure 3. Because the size and placement of the drawing template were determined on the basis of each participant's unique anthropometrics, averaged hand paths across participants would not be very informative of the changes across conditions. Here, we provide the data from 1 participant whose performance was representative. The data illustrate that the hand paths were always more circular when moving at the lowest frequency, and they became more elliptical when moving at the highest frequency. The distortion was most obvious for the nondominant (left) arm when drawing in the asymmetric pattern. Statistical analyses confirmed that there was a significant four-way interaction of Arm $\times$ Movement Pattern $\times$ Frequency, $F(3, 27) = 35.1, p < .001$. Circles produced by the nondominant arm became more like cigar-shaped ellipses, oriented toward 45° , when movement frequency increased, especially when performing the asymmetric pattern. Circles produced by the dominant arm were relatively more circular, although they tended to flatten more in the vertical direction as frequency increased (Figure 3).

Relative Variability of the Individual Hand Paths

We examined the CV of each hand's path in two dimensions to evaluate the consistency of movement performance across multiple cycles relative to the mean path. On average, the nondominant hand's path was more variable than that of the dominant hand, $F(1, 9) = 70.1, p < .001$. The change of variability depended on arm, movement pattern, and frequency, $F(3, 27) = 7.2, p = .001$. The CV for the dominant hand increased slightly and similarly for both symmetric and asymmetric drawing (Figure 4, two lower panels). In contrast, the CV for the nondominant arm increased substantially more with frequency, especially when drawing with the asymmetric pattern (Figure 4, two top panels). As a result, the difference in variability between two patterns of drawing was larger for the nondominant arm than for the dominant arm only when moving at higher frequencies, $F(1, 9) = 70.1, p < .01$, but not at lower frequencies, $p > .1$. There was no main effect or interaction effect associated with the template.

Variability of the Vector Difference Between Hands

Variability of the distance component of the vector difference between the hands (*SD*) increased with movement frequency, as revealed by a significant main effect of frequency, $F(3, 27) = 18.6, p < .001$. A significant Movement Pattern $\times$ Frequency interaction was also present, $F(3, 27) = 7.3, p < .05$, indicating that the increase in *SD* with frequency was greater when asymmetric drawing was performed than when symmetric drawing was performed (Figure 5, upper panel). A significant Template $\times$ Frequency interaction effect was also found, $F(3, 27) = 7.9, p < .01$; tracing the template resulted in a greater increase of the *SD* with frequency than did drawing without a template (Figure 5, upper panel), regardless of the movement pattern.

Variability of the directional component of the vector difference between the hands generally increased with movement frequency, $F(3, 27) = 13.0, p < .001$. A significant Movement Pattern $\times$ Frequency interaction revealed that that measure also increased more strongly with frequency

when drawing asymmetrically than it did when drawing symmetrically, $F(3, 27) = 8.0, p < .01$ (Figure 5, lower panel). A significant Template $\times$ Movement Pattern $\times$ Frequency interaction, $F(3, 27) = 10.2, p < .001$, resulted from a minimal difference in direction variability between the two template conditions during symmetrical and asymmetrical drawing; in the latter case, tracing the template at higher frequencies resulted in greater directional variability than did drawing a remembered circular pattern.

Joint Kinematics and Joint Excursion

The scapula and wrist were consistently involved in this drawing task, although their contribution was substantially less than that of the shoulder and elbow joints. Values of angular excursion for each joint during this circle-drawing task, averaged across conditions and participants, were $11.6^\circ \pm 1.02^\circ$ for the scapula, $35.7^\circ \pm 1.03^\circ$ for the shoulder, $54.1^\circ \pm 1.08^\circ$ for the elbow, and $7.9^\circ \pm 0.82^\circ$ for the wrist.

Joint Kinematics and Components of Joint Configuration Variance

Joint Configuration Variance Related to Control of Individual Hand Paths—

Overall joint configuration variance was higher for control of the nondominant hand's motion than for control of the dominant hand, $F(1, 9) = 15.2, p < .01$ (Figure 6, dotted lines). Collapsed across frequency, *NGEV* was higher with respect to control of the nondominant versus dominant hand's path, regardless of movement pattern: Symmetric pattern, $F(1, 9) = 2.8, p < .001$; asymmetric pattern, $F(1, 9) = 20.8, p < .001$ (Figure 6). There were also significant Arm $\times$ Frequency, $F(3, 27) = 14.2, p < .001$, and Arm $\times$ Movement Pattern $\times$ Frequency, $F(3, 27) = 3.1, p < .05$, interactions for *NGEV*. Tests of those interactions revealed two main findings. First, differences in *NGEV* between the arms were larger at higher (i.e., 2.0 and 2.5 Hz) than at lower (i.e., 1.0 and 1.5 Hz) frequencies, $F(1, 9) = 20.8, p = .001$. Second, the arm differences were similar for symmetric and asymmetric patterns, $p > .1$, when drawing at lower frequencies but differed significantly at the higher drawing frequencies, $F(1, 9) = 6.9, p < .05$. There were no apparent differences in *NGEV* between the two template conditions. The effect of template condition did not depend on the drawing pattern or the arm used to draw the circles.

The amount of *GEV* also increased with movement frequency, $F(3, 27) = 5.8, p < .01$ (see Figure 6, solid lines). For the symmetric pattern of bimanual drawing, *GEV* was not statistically different between the two arms, $p > .1$. However, *GEV* was significantly higher in the nondominant arm than in the dominant arm during asymmetric drawing, $F(1, 9) = 7.72, p < .05$. There was a significant Template $\times$ Frequency interaction for *GEV*, $F(1, 9) = 9.5, p < .05$, revealing that higher *GEV* was associated with drawing with the physical template at lower frequencies (with vs. without, respectively, $0.0040 \pm 0.0005 \text{ rad}^2$ vs. $0.0034 \pm 0.0005 \text{ rad}^2$) but not at higher frequencies (with vs. without, respectively, $0.0044 \pm 0.0006 \text{ rad}^2$ vs. $0.0045 \pm 0.0008 \text{ rad}^2$).

Joint Configuration Variance Related to Control of the Vector Difference

Between Two Hands—*GEV* was consistently higher than *NGEV* relative to controlling the vector difference between the hands when performing symmetric drawing but not for asymmetric drawing (Figure 7). Both components of variance revealed significant main effects of movement pattern—for *GEV*, $F(1, 9) = 10.3, p < .05$; for *NGEV*, $F(1, 9) = 16.8, p < .01$ —and frequency—for *GEV*, $F(3, 27) = 8.0, p = .01$; for *NGEV*, $F(3, 27) = 7.2, p = .01$. For *NGEV*, there was also a significant Pattern $\times$ Frequency interaction, $F(3, 27) = 5.3, p < .01$; *NGEV* during asymmetric drawing increased substantially over frequencies, whereas *NGEV* during symmetric drawing changed minimally, $F(1, 9) = 5.7, p < .05$. In addition, there was a significant Template $\times$ Movement Pattern $\times$ Frequency interaction, $F(3, 27) = 5.1, p < .01$, which resulted from the lower *NGEV* during asymmetric drawing without the template than during tracing of the template. That effect was present at the higher frequencies, $F(1, 9) = 6.2$,

$p < .05$, but not at the lower frequencies, $p > .1$. For *GEV*, a minimal difference in *GEV* accounted for a significant Template $\times$ Movement Pattern $\times$ Frequency interaction, $F(3, 27) = 4.9$, $p < .01$, when we compared the two template conditions during symmetrical drawing ($p > .1$) and asymmetric drawing; in the latter case, tracing the template at higher frequencies resulted in greater *GEV* than did drawing a remembered circular pattern, $F(1, 9) = 5.5$, $p < .05$.

Kinetic Analysis

Fragments of individual profiles of net (*NM*), interaction (*IM*), and muscle (*MM*) moments for each joint obtained during circle drawing with the dominant arm are shown in Figure 8. At the scapular and shoulder joints, *MM* was the dominant component in production of *NM*. At the elbow joint, however, both *IM* and *MM* contributed substantially to *NM*. At the wrist joint, *IM* and *MM* were of opposite sign and tended to cancel out each other, although a small *NM* was still present. Given that shoulder and elbow joints made the greatest contribution to the hands' motions in this task (see Joint Kinematics), we next focus the quantitative analysis on the shoulder and elbow joint dynamics.

Moment Signs—To better understand the role of muscular control in production of the shoulder and elbow motions, we analyzed the interval during which *MM* and *NM* had equal signs. When *NM* and *MM* share the same sign during the greatest proportion of the drawing cycle, the joint is likely accelerated mainly by muscular action. That proportion of sharing contrasted with a much shorter proportion of the cycle during which *MM* and *NM* were compatible; the latter proportion would indicate that *IM* played a more dominant role in accelerating that joint. The portion of cycle duration when *MM* acted to accelerate the shoulder was high for both arms, although the dominant shoulder's *MM* was less consistent with the *NM* during asymmetric than during symmetric drawing, $F(1, 9) = 16.5$, $p < .01$, as can be seen in Figure 9A. There was no difference between the two patterns for the nondominant arm ($p > .1$). For the dominant elbow joint, the relation of *MM* to *NM* was relatively constant across frequency steps, whereas *MM* was increasingly less consistent with *NM* with increasing frequency for the nondominant elbow joint, $F(3, 27) = 26.0$, $p < .001$ (Figure 9B).

Moment Impulse—The *MM* impulse of all joints increased with cycling frequency: For the scapula, shoulder, elbow, and wrist, respectively, $F_s(3, 27) = 70.6, 96.3, 50.2, 16.3$, all $ps < .001$. The *MM* impulse acted mostly to assist *NM*, as reflected by the positive values of *MM* impulse for all joints (only the elbow joint is shown). For the elbow joint (Figure 10A), there was a significant Arm $\times$ Movement Pattern $\times$ Frequency interaction, $F(3, 27) = 14.4$, $p < .001$. The effect indicated that the nondominant arm's *MM* impulse was smaller for asymmetric drawing than were the other Arm $\times$ Pattern combinations at all, $F(1, 9) = 28.8$, $p < .001$, but the lowest frequency, $p > .1$.

IM affected each joint differently. For the scapula, *IM* had a resistive effect (impulse range = -1.5 to -4.5 Nms; see Kinetic Analyses for definition of the sign of the moment), whereas *IM* had relatively small effects at the shoulder (range = -0.38 to 0.02 Nms) and at the wrist (range = 0.009 to -0.025 Nms) joints. At the elbow, *IM*, which arose mainly from the shoulder motion, on average assisted the *NM* (Figure 10B). That effect was reflected by positive values of *IM* impulse for all conditions. There was a significant Arm $\times$ Movement Pattern $\times$ Frequency interaction, $F(3, 27) = 16.7$, $p < .001$, which indicated that *IM* leveled off at higher frequencies during asymmetric drawing by the dominant arm. The dominant arm's *IM* impulse was smaller than any of the other combinations of arm and pattern (1.5–2.5-Hz) $F(1, 9) = 10.6$, $p = .01$. There was no difference between conditions, however, when moving at the lowest frequency (i.e., 1.0 Hz; $p < .1$).

Regression Analysis—For the nondominant arm, a linear regression analysis revealed that variability was significantly correlated with variability of the *IM* impulse ($r = .43$), $F(1, 158) = 36.8$, $p < .001$ (see Figure 11). No such correlation was found for drawing with the dominant arm ($p > .1$).

Discussion

Stability in the sense of nonlinear dynamics is the key concept in the dynamical systems perspective (Schöner & Kelso, 1988), that is, the notion that movement patterns emerge as stable states from the coupling of *dfs*. Transitions between patterns frequently occur through a loss of pattern stability under changing values of particular control parameters (Kelso, 1984). Most work based on a dynamical systems perspective has been concerned with the relative timing among limbs, among effectors, or between effectors and perceived external rhythms (reviewed in Schöner, 2002). The theory of the UCM shares that emphasis on stability, but postulates that patterns of elemental variables can be interpreted in terms of the stability of task-relevant variables (Schöner, 1995). Thus, the UCM approach deals specifically with how control of important performance variables is achieved through selective stabilization of particular directions in the space of the elemental variables. Within the UCM framework, the nervous system is hypothesized to take advantage of rather than restrict motor redundancy, a signature feature of biological systems, allowing for flexible movement control (Schöner, 1995; Scholz & Schöner, 1999). Results of the current experiment largely support both theoretical perspectives and provide new support for the UCM hypothesis in a rhythmic movement task.

As with previous studies of single-joint movements (Byblow et al., 2000; Kelso, 1984; Lee, Almeida, & Chua, 2002; Scholz & Kelso, 1989; Scholz et al., 1987) or other multi-*df* tasks (e.g., Byblow, Summers, Semjen, Wuyts, & Carson, 1999; Carson et al., 1997; Cattaert et al., 1999; Semjen et al., 1995; Serrien, Bogaerts, Suy, & Swinnen, 1999; Wuyts et al., 1996), the current experiments revealed through frequency scaling differences in the stability of the two hands' movement in relation to asymmetric and symmetric patterns of bimanual coordination. Hand-path variability was higher for the nondominant, left hand than for the dominant, right hand at all frequencies, and that difference was exacerbated at higher frequencies of circle drawing, particularly when performing the asymmetric pattern. That asymmetry in stability between the individual hand motions resulted in significant increases in the variability of the vector difference between the two hands during asymmetric drawing.

Control of Individual Hand Paths

An individual could accomplish a particular hand path during rhythmic circle drawing through the use of a relatively fixed sequence of joint combinations across repetitions. In that case, any variation of that combination would be expected to lead to increased variability of the hand path. Of course, in a nonredundant system, for example, two oscillating joints, joint motion is isomorphic with motion of the end-effector. For redundant systems, however, isomorphy does not need to be the case. According to the UCM theory, the motor system typically uses equivalent combinations of joint motions with respect to the hand's path (reflected by *GEV*) in a redundant system to produce a particular hand path, whereas it resists combinations of joint motion that lead to variability (reflected by *NGEV*). Results of the current experiment generally support that hypothesis for rhythmic movement, consistent with previous studies of discrete movement tasks (Reisman, Scholz, & Schöner, 2002; Scholz, Reisman, & Schöner, 2001; Scholz & Schöner, 1999; Scholz et al., 2000; Tseng et al., 2002; Tseng et al., 2003; Yang & Scholz, 2005). With respect to individual hand movements, combinations of joint motion that were equivalent with respect to producing the average hand path were, with few exceptions, substantially higher than were joint combinations leading to variability. When movement

frequency of the dominant hand increased, *NGEV* increased only slightly, whereas *GEV* increased even more. The increase in *NGEV* revealed the limits of restoring forces in directions of joint space that lead to variability. The increase in *GEV* revealed the UCM control strategy, allowing for flexible combinations of joint motions—that is, more than are strictly required—to achieve the hand's path. Coordination of the joints underlying control of the nondominant hand also revealed a UCM control strategy in that *GEV* increased with frequency when the task became more challenging. However, the limit of stability of coordinating the nondominant hand's *dfs* was revealed by the significantly greater increase in *NGEV* with frequency scaling. Whereas *NGEV* was relatively similar between the dominant and nondominant hands at the lowest movement frequency, it increased much more strongly with frequency in the nondominant hand, particularly for the asymmetric drawing pattern. Thus, the decrease in stability of the nondominant hand's movement during asymmetric drawing, depicted in Figure 4, was related to the weaker restoring forces acting to limit combinations of joint motions; the weakness of those forces would lead to variability of the hand path for control of the nondominant arm compared with that of the dominant arm.

Bimanual Coordination of *Df*: Symmetric Drawing

Achieving stable relative motion between the two hands could be the result of optimally controlling each individual hand's motion or could result from a common synergy that coordinates the joints across both limbs. Given that variability is a common feature of multi-*df* biological systems, a synergy uniting the joints of the two arms to achieve relative control is most likely (Kelso, 1984; Y. Li, Levin, Forner-Cordero, & Swinnen, 2005; Swinnen, 2002). The synergy leads to the possibility that relative control can conflict with individual control. When considering the symmetric mode of circle drawing, results of the current experiment suggest that a synergy uniting the two arms was given priority over the synergies controlling motion of each hand. That is, although both *GEV* and *NGEV* increased with frequency in relation to control of the individual hand paths (Figure 6), particularly for the nondominant arm, *GEV* and especially *NGEV* related to control of the vector difference between the hands' motions changed little with frequency (Figure 7). That effect for *GEV* depended more on whether participants drew a remembered or an actual circular template. The presence of a template appeared to limit the range of equivalent joint motions used to achieve the relative hand path, although *NGEV* was not much different (Figure 7, right and left panels). It is tempting to conclude that the slight increases in *NGEV* related to control of the dominant hand's path (Figure 6) reflected adjustments to compensate for variations of the nondominant hand's path, allowing the relative motion between the hands to remain fairly stable (Figure 7).

Bimanual Coordination of *Df*: Asymmetric Drawing

For asymmetric drawing, increases in *NGEV* related to control of the nondominant hand were apparently not as easily compensated, leading to significant increases in *NGEV* related to control of the relative motion between the hands and to poor bimanual motion stability (Figure 5). That was particularly true when participants traced a physical template. In that case, the conflict between keeping the spatial position of the individual hand paths coincident with the physical templates and maintaining consistent relative motion between the two hands was clearly apparent (see the following comments). The result for asymmetric drawing reflected the fact that the synergy uniting nonhomologous muscles across the two arms is less stable than is the synergy uniting homologous muscles in the symmetric pattern (Y. Li et al., 2005; Swinnen et al., 1998). In fact, neurophysiologic evidence has shown that differences in the organization of neural activity may account for differences in the effect of frequency scaling on the symmetric and asymmetric patterns (Mayville, Bressler, Fuchs, & Kelso, 1999; Ullen, Forssberg, & Ehrsson, 2003; for a review, also see Swinnen & Wenderoth, 2004). With increases in movement frequency, the degree of simultaneous activation of both hemispheres

has been shown to decrease when individuals perform an asymmetric movement, whereas no obvious decrease was found for a symmetric movement (Serrien & Brown, 2002).

Despite the obvious decrease of stability of the asymmetric drawing pattern with increasing frequency, we did not observe a switch from that pattern to the more stable symmetric drawing pattern. That finding is not surprising, given that circle drawing also failed to show pattern transitions in most previous studies (Byblow et al., 1999; Carson et al., 1997; Semjen et al., 1995; Wuyts et al., 1996). On the other hand, other investigators have argued that other parameters besides movement frequency may influence pattern transitions in circle-drawing tasks. For example, reducing the size of circles drawn, and, consequently, shoulder and elbow joint amplitudes, was shown to systematically change pattern stability as well as the likelihood of pattern transitioning even though movement frequency was fixed (Ryu & Buchanan, 2004). Moreover, the nature of available tactile information also appears to influence the stability of coordination patterns. Pattern transitioning was more likely to occur when participants were required to trace circles while holding a stylus than when they used their fingers to perform the tracing task (Buchanan & Ryu, 2005).

Another possible account for the absence of pattern transitions, however, is that the availability of additional *dfs* can delay the transition from a typically less stable pattern into a more stable pattern by recruiting those additional *dfs* into the task (Buchanan & Kelso, 1999; Fink, Kelso, Jirsa, & DeGuzman, 2000). Thus, the motor system uses more of the available *dfs* when maintenance of the pattern becomes more difficult at higher frequencies. Evidence for that fact was provided by the observed increase in *GEV* related to the control of individual hand paths. Thus, although additional individual *dfs* were not recruited in this experiment—that is, all eight joints participated in the task at all frequencies—more combinations of the available *dfs* were used to stabilize the hand's movement path and the vector difference between the hands. Nonetheless, the fact that *NGEV* also increased with frequency with respect to control of the nondominant hand and the vector difference during asymmetric drawing indicates that the recruitment of *dfs* was not always selective or adequate.

Effect of Tracing a Spatial Template During Circle Drawing

When participants performed bimanual asymmetric circle drawing, both components of joint configuration variance related to control of the vector difference between the two hands increased with frequency. The increase in the variance components tended to occur in parallel when drawing without a physical template. When the physical template was traced in the asymmetric pattern, however, the component of variance leading to errors in the vector difference between the hands increased more with frequency than did the component of variance that reflected equivalent solutions to joint coordination, and the value of those components was significantly higher in the template than in the no-template condition (Figure 7). The reason for the difference may be that tracing a template required performance of a secondary task and, presumably, demanded greater attention, which was not a factor when the remembered template was drawn. In the template condition, participants required hand–eye coordination to keep each hand on its individual template. That form of coordination may make it easier for individuals to maintain the spatial relationship between the hands but could be more challenging to maintaining the appropriate temporal coordination. In comparison, when participants were asked to trace the remembered template, that task did not require the same degree of online eye–hand coordination. As a result, maintaining the bimanual relationship could be expected to be easier in the no-template condition, which was the case. On the other hand, the difference between the template and no-template conditions resulted in a less substantial influence on the control of the individual hand's path. Thus, when drawing the template, participants apparently gave more attention to accurately tracing the template than to maintaining the appropriate interlimb coordination pattern. Although that difference

between template and no-template conditions was not a major factor when participants cycled the hands symmetrically, it became more of a problem when they performed asymmetric circle drawing. Tracking of eye movements in future studies of this task will be necessary to enable investigators to better understand the factors leading to that difference.

Biomechanical Influences on the Frequency and Pattern Effects

Intersegmental dynamics has an important effect on movement production and must be accounted for by the nervous system (for a review, see Ketcham, Dounskaia, & Stelmach, 2004). Moreover, the system's ability to account for intersegmental dynamics appears to be arm dependent (Sainburg & Kalakanis, 2000). Given that fact, one can expect that imbalance to affect the ability to coordinate the two hands' motions in bimanual tasks. In the present experiment, the difference in intersegmental dynamics between the arms was observed primarily at the elbow joint, and much less so at the scapular, shoulder, or wrist joints. Moreover, the difference was limited to the asymmetric pattern of circle drawing. When the muscle and interaction moments of the elbow were similar across the arms during symmetric circle drawing, performance of that bimanual drawing task was relatively stable, as reflected by consistent individual hand paths and the vector difference between the two hands.

During asymmetric drawing, however, there appeared to be an imbalance between the two arms in how participants dealt with the interaction moment. First, the *IM* impulse continued to increase with movement frequency in the nondominant arm, whereas the *IM* contribution increased much less with frequency in the dominant arm, and the difference between the arms became greater with increasing cycling frequency (Figure 10). Second, the contribution of muscular control was just the opposite; the *MM* impulse increased in the dominant arm during frequency scaling, as it did in symmetric drawing. However, a decreased role of muscle control was apparent with increasing frequency in the nondominant arm during asymmetric drawing. Both findings point to differences in the control of the two arms. The greater influence of *IM* than *MM* in the nondominant arm may be related to the observed increase in *NGEV* for the nondominant arm and its more variable hand path. That is, *IM* predominantly accelerated the movement, and the acceleration apparently led to errors in the required hand path. That interpretation is consistent with that of a previous study reporting the effect of *IMs* on the stability of interjoint coordination (Dounskaia et al., 1998). The results indicated that when movement frequency was high, the interaction forces from the proximal elbow joint dominated motions of the distal wrist joint in a two-joint rhythmic task, leading to a changed pattern of interjoint coordination.

Previous studies have shown that the efficiency of using intersegmental forces is arm dependent during reaching tasks (Bagesteiro & Sainburg, 2002; Sainburg & Kalakanis, 2000). Those results demonstrated that when the interaction moment was not fully accounted for, that would lead to a curvature in the hand path, which was found only for the nondominant arm. In contrast, control of the dominant hand's path was independent of the magnitude of the interaction moment because of a more efficient coordination between the interaction and muscular forces (Sainburg & Kalakanis). Our results in this bimanual circle-drawing task partially support the findings of Sainburg and colleagues. However, the current experiment did not reveal the same purported efficiency of intersegmental dynamics in the dominant arm, as shown by higher *IM* and lower *MM* as reported (Bagesteiro & Sainburg; Sainburg & Kalakanis). Nonetheless, cycle-to-cycle variability of the nondominant hand's path was significantly related to the variability of the elbow's *IM* impulse in the current experiment (Figure 11). Moreover, that relationship was not found for the dominant arm, suggesting that control of the dominant arm was far less influenced by the intersegmental interactions. A number of factors may account for the fact that the current results are not fully consistent with the results of Sainburg and colleagues. First, in the current study, we examined a redundant task, unlike the task used in

the studies of Sainburg and colleagues. Available motor redundancy may allow for some dissipation of the effects of *IMs* by enabling compensatory adjustment at other joints so that these effects of redundancy on end-effector movement are minimized, consistent with the idea of error compensation (Latash, Danion, Scholz, Zatsiorsky, & Schöner, 2003). When abundant joint combinations are not available, deviation from a planned joint trajectory because of the unexpected or inadequate planning for the effect of *IMs* would inevitably lead to errors in performance. Second, in previous studies revealing differences between the arms, investigators did not look at tasks that required coupling of the two hand's movement. Third, discrete and rhythmic movements are known to have different kinematic properties (van Mourik & Beek, 2004) and may be controlled via different neural dynamics (Sternad, Dean, & Schaal, 2000). Therefore, the observed differences in the arms' dynamics compared with those in previous reports require further investigation, perhaps using bilateral reaching tasks with different interlimb patterns.

An alternative explanation for the observed difference of joint moments between the two arms during asymmetric drawing could be related to the instantaneous difference in arm configurations of the two arms when compared with that in symmetric drawing. During bimanual symmetric drawing, the two arms exhibit similar configurations at every instant in time across the drawing cycle (Figure 1B). Thus, muscle activations should be comparable between the two arms throughout the movement. As a result, it may be easier for the nervous system to maintain the desired temporal coordination between the actions of the two arms because the control of both arms can be more easily united. In contrast, the arm configurations were substantially different from instant to instant between the arms when bimanual asymmetric drawing was performed (Figure 1C), which likely posed more difficulty in uniting control of the two arms. In fact, stronger interhemispheric coupling appears to be necessary when the asymmetric pattern is performed than is needed when the symmetric pattern is performed (Cardoso de Oliveira, Gribova, Donchin, Bergman, & Vaadia, 2001; Serrien & Brown, 2002), suggesting that more brain resources must be recruited when the more difficult asymmetric pattern is performed (Mayville et al., 1999). However, the difference in joint configurations between the drawing patterns is unlikely to be the primary factor leading to the differences in joint moments observed here, because the *NM* and *MM* impulses did not differ between the arms during asymmetric drawing at the lower frequencies despite differences in instantaneous arm configuration. Thus, coordinating two effectors that require different muscular actions may become more problematic at higher frequencies.

Conclusion

This study revealed for the first time how previously reported frequency-related changes in bimanual coordination of two arms with redundant joint motions are related to differences in the selective use of equivalent solutions to coordinating the joints. Variations of the joint configuration across repetitions of drawing were more likely to reflect joint configurations that were equivalent with respect to producing the same average hand path or relative position and orientation of the two hands than to reflect error variance, that is, $GEV \gg NGEV$, supporting the UCM hypothesis. The effect differed, however, with respect to control of the dominant and nondominant arms and was strongly influenced by the pattern of bimanual movement performed. For the symmetric pattern of drawing, in which homologous muscle groups across two arms were used, control of both arms was associated with a higher amount of goal-equivalent than non-goal-equivalent joint configuration variance at all frequencies, even though overall variance was higher for the nondominant arm. The same relationship between *GEV* and *NGEV* held for the dominant arm when the asymmetric drawing pattern was performed. However, the nondominant arm demonstrated a relatively greater increase of the *NGEV* with increasing frequency. The observed difference in joint coordination between the arms and, subsequently, in the stability of individual and relative hand movement across

drawing patterns, appeared to be related to differences between the arms in the effect of intersegmental dynamics. The effects of *IM* and *MM* were found to be similar across the two arms when the symmetric drawing pattern was performed. However, control of the nondominant arm was more dominated by the *IM* and was less related to the *MM* than was that of the dominant arm when asymmetric circle drawing was performed. Thus, our results suggest that differences between the dominant and nondominant arms' kinetic characteristics are not absolute but are related to the nature of their bimanual coupling. The requirement to follow a predefined template also affected the selective use of goal-equivalent joint combinations to stabilize the relative position and orientation of the two hands. That effect may have resulted from the added demand on attention of keeping the individual hands on the physical template while maintaining a consistent relationship between the two hands when tracing an actual template compared with the attentional demands during the drawing of a remembered template, rather than from biomechanical factors.

ACKNOWLEDGMENT

Grants IBN0078127 from the National Science Foundation and NS-50880 from the National Institutes of Health awarded to J. P. Scholz supported this study. We thank an anonymous reviewer and John Buchanan for their many helpful suggestions and comments provided on an earlier draft of this manuscript.

APPENDIX

The individual terms of the M matrix and the H matrices are listed in the following. Note that the diagonal terms are $M_{1,1}$, $M_{2,2}$, $M_{3,3}$, and $M_{4,4}$, whereas the off-diagonal terms are $M_{i,j}$, where $i \neq j$; i and $j = 1, 2, 3$, and 4 . The same arrangement applies to the H vector. Notation: θ_i = angle of the i th joint; l_i = length of the i th segment; r_i = position of the center of mass of the i th segment from the proximal end of that segment; m_i = mass of the i th segment; and segment I_i = moment of inertia of the i th segment. The numbers 1, 2, 3, and 4 represent each arm segment and joint angle, that is, the clavicle (scapula), upper arm (shoulder), forearm (elbow), and hand (wrist), respectively.

$$\begin{aligned}
 M(\theta)_{1,1} = & I_1 + I_2 + I_3 + I_4 + m_1 \cdot r_1^2 + (m_2 + m_3 + m_4) \cdot l_1^2 + (m_3 + m_4) \cdot l_2^2 + m_2 \cdot r_2^2 + m_4 \cdot l_3^2 \\
 & + m_3 \cdot r_3^2 + m_4 \cdot r_4^2 + m_3 \cdot [2 \cdot l_1 \cdot l_2 \cdot \cos(\theta_2) + 2 \cdot l_1 \cdot r_3 \cdot \cos(\theta_2 + \theta_3) + 2 \cdot l_2 \cdot r_3 \cdot \cos(\theta_3)] \\
 & + 2 \cdot m_2 \cdot l_1 \cdot r_2 \cos(\theta_2) + m_4 \cdot [2 \cdot l_1 \cdot l_2 \cdot \cos(\theta_2) + 2 \cdot l_1 \cdot l_3 \cdot \cos(\theta_2 + \theta_3) + 2 \cdot l_1 \cdot r_4 \\
 & \cdot \cos(\theta_2 + \theta_3 + \theta_4) + 2 \cdot l_2 \cdot l_3 \cdot \cos(\theta_3) + 2 \cdot l_2 \cdot r_4 \cdot \cos(\theta_3 + \theta_4) + 2 \cdot l_3 \cdot r_4 \cdot \cos(\theta_4)].
 \end{aligned} \tag{A1}$$

$$\begin{aligned}
 M(\theta)_{1,2} = & I_2 + I_3 + I_4 + m_2 \cdot r_2^2 + m_3 \cdot r_3^2 + m_4 \cdot r_4^2 + m_2 \cdot l_1 \cdot r_2 \cdot \cos(\theta_2) + (m_3 + m_4) \cdot l_2^2 + m_4 \cdot l_3^2 + m_3 \\
 & \cdot [l_1 \cdot l_2 \cdot \cos(\theta_2) + l_1 \cdot r_3 \cdot \cos(\theta_2 + \theta_3) + 2 \cdot l_2 \cdot r_3 \cdot \cos(\theta_3)] + m_4 \cdot [l_1 \cdot l_2 \cdot \cos(\theta_2) + l_1 \cdot l_3 \cdot \cos(\theta_2 + \theta_3) \\
 & + l_1 \cdot r_4 \cdot \cos(\theta_2 + \theta_3 + \theta_4) + 2 \cdot l_2 \cdot l_3 \cdot \cos(\theta_3) + 2 \cdot l_2 \cdot r_4 \cdot \cos(\theta_3 + \theta_4) + 2 \cdot l_3 \cdot r_4 \cdot \cos(\theta_4)].
 \end{aligned} \tag{A2}$$

$$\begin{aligned}
 M(\theta)_{1,3} = & I_3 + I_4 + m_3 \cdot r_3^2 + m_4 \cdot r_4^2 + m_4 \cdot l_3^2 + m_3 \cdot [l_1 \cdot r_3 \cdot \cos(\theta_2 + \theta_3) + l_2 \cdot r_3 \cdot \cos(\theta_3)] + m_4 \\
 & \cdot [l_1 \cdot l_3 \cdot \cos(\theta_2 + \theta_3) + l_1 \cdot r_4 \cdot \cos(\theta_2 + \theta_3 + \theta_4) + l_2 \cdot l_3 \cdot \cos(\theta_3) + l_2 \cdot r_4 \cdot \cos(\theta_3 + \theta_4) \\
 & + 2 \cdot l_3 \cdot r_4 \cdot \cos(\theta_4)].
 \end{aligned} \tag{A3}$$

$$M(\theta)_{1,4} = I_4 + m_4 \cdot r_4^2 + m_4 [l_1 \cdot r_4 \cdot \cos(\theta_2 + \theta_3 + \theta_4) + l_2 \cdot r_4 \cdot \cos(\theta_3 + \theta_4) + l_3 \cdot r_4 \cdot \cos(\theta_4)]. \tag{A4}$$

$$M(\theta)_{2,1} = M(\theta)_{1,2}. \tag{A5}$$

$$M(\theta)_{2,2} = I_2 + I_3 + I_4 + m_2 \cdot r_2^2 + m_3 \cdot l_2^2 + m_3 \cdot r_3^2 + 2 \cdot m_3 \cdot l_2 \cdot r_3 \cdot \cos(\theta_3) + m_4 \cdot [l_2^2 + l_3^2 + r_4^2 + 2 \cdot l_2 \cdot l_3 \cdot \cos(\theta_3) + 2 \cdot l_2 \cdot r_4 \cdot \cos(\theta_3 + \theta_4) + 2 \cdot l_3 \cdot r_4 \cdot \cos(\theta_4)] \quad (A6)$$

$$M(\theta)_{2,3} = I_4 + I_3 + m_3 \cdot r_3^2 + m_3 \cdot l_2 \cdot r_3 \cdot \cos(\theta_3) + m_4 \cdot [l_3^2 + r_4^2 + l_2 \cdot l_3 \cdot \cos(\theta_3) + l_2 \cdot r_4 \cdot \cos(\theta_3 + \theta_4) + 2 \cdot l_3 \cdot r_4 \cdot \cos(\theta_4)] \quad (A7)$$

$$M(\theta)_{2,4} = I_4 + m_4 \cdot r_4^2 \cdot l_2 + r_4 \cdot \cos(\theta_3 + \theta_4) + m_4 \cdot l_3 \cdot r_4 \cdot \cos(\theta_4) \quad (A8)$$

$$M(\theta)_{3,1} = M(\theta)_{1,3} \quad (A9)$$

$$M(\theta)_{3,2} = M(\theta)_{2,3} \quad (A10)$$

$$M(\theta)_{3,3} = I_3 + I_4 + m_3 \cdot r_3^2 + m_4 \cdot [l_3^2 + r_4^2 + 2 \cdot l_3 \cdot r_4 \cdot \cos(\theta_4)] \quad (A11)$$

$$M(\theta)_{3,4} = I_4 + m_4 \cdot r_4^2 + m_4 \cdot l_3 \cdot r_4 \cdot \cos(\theta_4) \quad (A12)$$

$$M(\theta)_{4,1} = M(\theta)_{1,4} \quad (A13)$$

$$M(\theta)_{4,2} = M(\theta)_{2,4} \quad (A14)$$

$$M(\theta)_{4,3} = M(\theta)_{3,4} \quad (A15)$$

$$M(\theta)_{4,4} = m_4 \cdot r_4^2 + I_4 \quad (A16)$$

$$\begin{aligned} H(\theta, \dot{\theta})_1 = & \left(2 \cdot \dot{\theta}_1 \cdot \dot{\theta}_3 + 2 \cdot \dot{\theta}_2 \cdot \dot{\theta}_3 + \dot{\theta}_3^2 \right) \cdot \left[-m_3 \cdot l_1 \cdot r_3 \cdot \sin(\theta_2 + \theta_3) - m_3 \cdot l_2 \cdot r_3 \cdot \sin(\theta_3) \right] + \left(\dot{\theta}_2^2 + 2 \cdot \dot{\theta}_1 \cdot \dot{\theta}_2 \right) \\ & \cdot \left[\sin(\theta_2) \cdot \left(-m_2 \cdot l_1 \cdot r_2 - m_3 \cdot l_1 \cdot l_2 \right) - m_3 \cdot l_1 \cdot r_3 \cdot \sin(\theta_2 + \theta_3) \right] - m_4 \cdot \left[\left(2 \cdot \dot{\theta}_1 \cdot \dot{\theta}_4 + 2 \cdot \dot{\theta}_2 \cdot \dot{\theta}_4 \right. \right. \\ & + 2 \cdot \dot{\theta}_3 \cdot \dot{\theta}_4 + \dot{\theta}_4^2 \cdot \left. \left(l_3 \cdot r_4 \cdot \sin(\theta_4) + l_2 \cdot r_4 \cdot \sin(\theta_3 + \theta_4) + l_1 \cdot r_4 \cdot \sin(\theta_2 + \theta_3 + \theta_4) \right) \right] + \left(2 \cdot \dot{\theta}_1 \cdot \dot{\theta}_3 \right. \\ & + 2 \cdot \dot{\theta}_2 \cdot \dot{\theta}_3 + \dot{\theta}_3^2 \cdot \left. \left(l_2 \cdot r_4 \cdot \sin(\theta_3 + \theta_4) + l_1 \cdot l_3 \cdot \sin(\theta_2 + \theta_3) + l_2 \cdot l_3 \cdot \sin(\theta_3) + l_1 \cdot r_4 \right. \right. \\ & \cdot \left. \sin(\theta_2 + \theta_3 + \theta_4) \right) + \left(2 \cdot \dot{\theta}_1 \cdot \dot{\theta}_2 + \dot{\theta}_2^2 \right) \cdot \left[l_1 \cdot r_4 \cdot \sin(\theta_2 + \theta_3 + \theta_4) + l_1 \cdot l_3 \cdot \sin(\theta_2 + \theta_3) \right. \\ & \left. \left. + l_1 \cdot l_2 \cdot \sin(\theta_2) \right] \right] \quad (A17) \end{aligned}$$

$$\begin{aligned} H(\theta, \dot{\theta})_2 = & \dot{\theta}_1^2 \cdot \sin(\theta_2) \cdot \left(m_2 \cdot l_1 \cdot r_2 + m_3 \cdot l_1 \cdot l_2 \right) + m_3 \cdot r_3 \cdot l_1 \cdot \sin(\theta_2 + \theta_3) \cdot \dot{\theta}_1^2 - m_3 \cdot l_2 \cdot r_3 \cdot \sin(\theta_3) \\ & \cdot \left(2 \cdot \dot{\theta}_3 \cdot \dot{\theta}_1 + 2 \cdot \dot{\theta}_3 \cdot \dot{\theta}_2 + \dot{\theta}_3^2 \right) + \dot{\theta}_1^2 \cdot \left[m_4 \cdot l_1 \cdot l_2 \cdot \sin(\theta_2) + m_4 \cdot l_1 \cdot l_3 \cdot \sin(\theta_2 + \theta_3) + m_4 \cdot l_1 \cdot r_4 \right. \\ & \cdot \left. \sin(\theta_2 + \theta_3 + \theta_4) \right] - m_4 \cdot \left[\left(l_2 \cdot l_3 \cdot \sin(\theta_3) + l_2 \cdot r_4 \cdot \sin(\theta_3 + \theta_4) \right) \cdot \left(2 \cdot \dot{\theta}_3 \cdot \dot{\theta}_1 + 2 \cdot \dot{\theta}_3 \cdot \dot{\theta}_2 + \dot{\theta}_3^2 \right) \right. \\ & \left. \left. + \left(l_2 \cdot r_4 \cdot \sin(\theta_3 + \theta_4) + l_3 \cdot r_4 \cdot \sin(\theta_4) \right) \cdot \left(2 \cdot \dot{\theta}_1 \cdot \dot{\theta}_4 + 2 \cdot \dot{\theta}_2 \cdot \dot{\theta}_4 + 2 \cdot \dot{\theta}_3 \cdot \dot{\theta}_4 + \dot{\theta}_4^2 \right) \right] \right] \quad (A18) \end{aligned}$$

$$\begin{aligned}
H(\theta, \dot{\theta})_3 &= \left(\dot{\theta}_1^2 + \dot{\theta}_2^2 + 2 \cdot \dot{\theta}_1 \cdot \dot{\theta}_2 \right) \cdot \left[m_3 \cdot l_2 \cdot r_3 \cdot \sin(\theta_3) + m_4 \cdot l_2 \cdot l_3 \cdot \sin(\theta_3) + m_4 \cdot l_2 \cdot r_4 \cdot \sin(\theta_3 + \theta_4) \right] \\
&+ \dot{\theta}_1^2 \cdot \left[m_3 \cdot l_1 \cdot r_3 \cdot \sin(\theta_2 + \theta_3) + m_4 \cdot l_1 \cdot l_3 \cdot \sin(\theta_2 + \theta_3) + m_4 \cdot l_1 \cdot r_4 \cdot \sin(\theta_2 + \theta_3 + \theta_4) \right] \\
&- m_4 \cdot l_3 \cdot r_4 \cdot \sin(\theta_4) \cdot \left(2 \cdot \dot{\theta}_4 \cdot \dot{\theta}_1 + 2 \cdot \dot{\theta}_4 \cdot \dot{\theta}_2 + 2 \cdot \dot{\theta}_4 \cdot \dot{\theta}_3 + \dot{\theta}_4^2 \right).
\end{aligned} \tag{A19}$$

$$\begin{aligned}
H(\theta, \dot{\theta})_4 &= \dot{\theta}_1^2 \cdot m_4 \cdot l_1 \cdot r_4 \cdot \sin(\theta_2 + \theta_3 + \theta_4) + \left(\dot{\theta}_1 + \dot{\theta}_2 \right)^2 \cdot m_4 \cdot l_2 \cdot r_4 \cdot \sin(\theta_3 + \theta_4) + m_4 \cdot l_3 \cdot r_4 \cdot \sin(\theta_4) \\
&\cdot \left[\left(\dot{\theta}_1 + \dot{\theta}_2 \right)^2 + 2 \cdot \dot{\theta}_1 \cdot \dot{\theta}_3 + 2 \cdot \dot{\theta}_2 \cdot \dot{\theta}_3 + \dot{\theta}_3^2 \right].
\end{aligned} \tag{A20}$$

REFERENCES

- Abbs JH, Gracco VL, Blair C. Functional muscle partitioning during voluntary movement: Facial muscle activity for speech. *Experimental Neurology* 1984;85:469–479. [PubMed: 6468573]
- Bagesteiro LB, Sainburg RL. Handedness: Dominant arm advantages in control of limb dynamics. *Journal of Neurophysiology* 2002;88:2408–2421. [PubMed: 12424282]
- Bastian AJ, Martin TA, Keating JG, Thach WT. Cerebellar ataxia: Abnormal control of interaction torques across multiple joints. *Journal of Neurophysiology* 1996;76:492–509. [PubMed: 8836239]
- Beer RF, Dewald JPA, Rymer WZ. Deficits in the coordination of multijoint arm movements in patients with hemiparesis: Evidence for disturbed control of limb dynamics. *Experimental Brain Research* 2000;131:305–319.
- Buchanan JJ, Kelso JAS. To switch or not to switch: Recruitment of degrees of freedom stabilizes biological coordination. *Journal of Motor Behavior* 1999;31:126–144. [PubMed: 11177627]
- Buchanan JJ, Ryu YU. The interaction of tactile information and movement amplitude in a multijoint bimanual circle-tracing task: Phase transitions and loss of stability. *The Quarterly Journal of Experimental Psychology* 2005;58A:769–787. [PubMed: 16194935]
- Byblow WD, Lewis GN, Stinear JW, Austin NJ, Lynch M. The subdominant hand increases the efficacy of voluntary alterations in bimanual coordination. *Experimental Brain Research* 2000;131:366–374.
- Byblow WD, Summers JJ, Semjen A, Wuyts IJ, Carson RG. Spontaneous and intentional pattern switching in a multisegmental bimanual coordination task. *Motor Control* 1999;3:372–393. [PubMed: 10529502]
- Cardoso de Oliveira S, Gribova A, Donchin O, Bergman H, Vaadia E. Neural interactions between motor cortical hemispheres during bimanual and unimanual arm movements. *The European Journal of Neuroscience* 2001;14:1881–1896. [PubMed: 11860483]
- Carson RG, Thomas J, Summers JJ, Walters MR, Semjen A. The dynamics of bimanual circle drawing. *The Quarterly Journal of Experimental Psychology* 1997;50A:664–683. [PubMed: 9314729]
- Cattaert D, Semjen A, Summers JJ. Simulating a neural cross-talk model for between-hand interference during bimanual circle drawing. *Biological Cybernetics* 1999;81:343–358. [PubMed: 10541937]
- Desmurget M, Prablanc C, Rossetti Y, Arzi M, Paulignan Y, Urquizar C, et al. Postural and synergic control for three-dimensional movements of reaching and grasping. *Journal of Neurophysiology* 1995;74:905–910. [PubMed: 7472395]
- Domkin D, Laczko J, Jaric S, Johansson H, Latash ML. Structure of joint variability in bimanual pointing tasks. *Experimental Brain Research* 2002;143:11–23.
- Dounskaia NV, Swinnen SP, Walter CB, Spaepen AJ, Verschueren SMP. Hierarchical control of different elbow-wrist coordination patterns. *Experimental Brain Research* 1998;121:239–254.
- Feldman AC. Once more on the equilibrium-point hypothesis (λ model) for motor control. *Journal of Motor Behavior* 1986;18:17–54. [PubMed: 15136283]
- Fink PW, Kelso JAS, Jirsa VK, DeGuzman G. Recruitment of degrees of freedom stabilizes coordination. *Journal of Experimental Psychology: Human Perception and Performance* 2000;26:671–692. [PubMed: 10811169]
- Gelfand IM, Latash ML. On the problem of adequate language in movement science. *Motor Control* 1998;2:306–313. [PubMed: 9758883]

- Ghez C, Gordon J, Ghilardi MF. Impairments of reaching movements in patients without proprioception. II. Effects of visual information on accuracy. *Journal of Neurophysiology* 1995;73:361–372. [PubMed: 7714578]
- Hanavan, EP. A mathematical model of the human body (Tech. Rep. No. AMRL-TR-102). Wright-Patterson Air Force Base, Aerospace Medical Research Libraries; Dayton, OH: 1964.
- Hogan N. The mechanics of multi-joint posture and movement control. *Biological Cybernetics* 1985;52:315–331. [PubMed: 4052499]
- Hollerbach JM, Flash T. Dynamic interactions between limb segments during planar arm movement. *Biological Cybernetics* 1982;44:67–77. [PubMed: 7093370]
- Kelso JAS. Phase transitions and critical behavior in human bimanual coordination. *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology* 1984;246:R1000–R1004.
- Ketcham CJ, Dounskaia NV, Stelmach GE. Multijoint movement control: The importance of interactive torques. *Progress in Brain Research* 2004;143:207–218. [PubMed: 14653166]
- Krishnamoorthy V, Yang J, Scholz JP. Joint coordination during quiet stance: Effects of vision. *Experimental Brain Research* 2005;164:1–17.
- Latash ML, Danion F, Scholz JP, Zatsiorsky VM, Schöner G. Approaches to analysis of handwriting as a task of coordinating a redundant motor system. *Human Movement Science* 2003;22:153–171. [PubMed: 12667747]
- Latash ML, Scholz JP, Danion F, Schöner G. Structure of motor variability in marginally redundant multifinger force production tasks. *Experimental Brain Research* 2001;141:153–165.
- Latash ML, Scholz JF, Danion F, Schöner G. Finger coordination during discrete and oscillatory force production tasks. *Experimental Brain Research* 2002;146:419–432.
- Lee TD, Almeida QJ, Chua R. Spatial constraints in bimanual coordination: Influences of effector orientation. *Experimental Brain Research* 2002;146:205–212.
- Li Y, Levin O, Forner-Cordero A, Swinnen SP. Interactions between interlimb and intralimb coordination during the performance of bimanual multijoint movements. *Experimental Brain Research* 2005;163:515–526.
- Li ZM, Latash ML, Zatsiorsky VM. Force sharing among fingers as a model of the redundancy problem. *Experimental Brain Research* 1998;119:276–286.
- Macpherson JM, Rushmer DS, Dunbar DC. Postural responses in the cat to unexpected rotations of the supporting surface: Evidence for a centrally generated synergic organization. *Experimental Brain Research* 1986;62:152–160.
- Mayville JM, Bressler SL, Fuchs A, Kelso JA. Spatiotemporal reorganization of electrical activity in the human brain associated with a timing transition in rhythmic auditory-motor coordination. *Experimental Brain Research* 1999;127:371–381.
- Medendorp WP, Crawford JD, Henriques DY, Van Gisbergen JA, Gielen CC. Kinematic strategies for upper arm-forearm coordination in three dimensions. *Journal of Neurophysiology* 2000;84:2302–2316. [PubMed: 11067974]
- Murray, R.; Li, Z.; Sastry, SS. A mathematical introduction to robotic manipulation. CRC Press; Boca Raton, FL: 1994.
- Oldfield RC. The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia* 1971;9:97–113. [PubMed: 5146491]
- Pelz J, Hayhoe M, Loeber R. The coordination of eye, head, and hand movements in a natural task. *Experimental Brain Research* 2001;139:266–277.
- Reisman DS, Scholz JP, Schöner G. Coordination underlying the control of whole body momentum during sit-to-stand. *Gait and Posture* 2002;15:45–55. [PubMed: 11809580]
- Ryu YU, Buchanan JJ. Amplitude scaling in a bimanual circle-drawing task: Pattern switching and end-effector variability. *Journal of Motor Behavior* 2004;36:265–279. [PubMed: 15262623]
- Sainburg RL, Ghilardi MF, Poizner H, Ghez C. Control of limb dynamics in normal subjects and patients without proprioception. *Journal of Neurophysiology* 1995;73:820–835. [PubMed: 7760137]
- Sainburg RL, Kalakanis D. Differences in control of limb dynamics during dominant and nondominant arm reaching. *Journal of Neurophysiology* 2000;83:2661–2675. [PubMed: 10805666]

- Santello M, Soechting JF. Force synergies for multi-fingered grasping. *Experimental Brain Research* 2000;133:457–467.
- Scholz JP, Danion F, Latash ML, Schöner G. Understanding finger coordination through analysis of the structure of force variability. *Biological Cybernetics* 2002;86:29–39. [PubMed: 11918210]
- Scholz JP, Kelso JAS. A quantitative approach to understanding the formation and change of coordinated movement patterns. *Journal of Motor Behavior* 1989;21:122–144. [PubMed: 15132941]
- Scholz JP, Kelso JAS, Schöner G. Nonequilibrium phase transitions in coordinated biological motion: Critical slowing down and switching time. *Physics Letters A* 1987;124:390–394.
- Scholz JP, Reisman D, Schöner G. Effects of varying task constraints on solutions to joint coordination in a sit-to-stand task. *Experimental Brain Research* 2001;141:485–500.
- Scholz JP, Schöner G. The uncontrolled manifold concept: Identifying control variables for a functional task. *Experimental Brain Research* 1999;126:289–306.
- Scholz JP, Schöner G, Latash ML. Identifying the control structure of multijoint coordination during pistol shooting. *Experimental Brain Research* 2000;135:382–404.
- Schöner G. Recent developments and problems in human movement science and their conceptual implications. *Ecological Psychology* 1995;7:291–314.
- Schöner G. Timing, clocks, and dynamical systems. *Brain and Cognition* 2002;48:31–51. [PubMed: 11812031]
- Schöner G, Kelso JA. Dynamic pattern generation in behavioral and neural systems. *Science* 1988;239(4847):1513–1520. [PubMed: 3281253]
- Semjen A, Summers JJ, Cattaert D. Hand coordination in bimanual circle drawing. *Journal of Experimental Psychology: Human Perception and Performance* 1995;21:1139–1157.
- Serrien DJ, Bogaerts H, Suy E, Swinnen SP. The identification of coordination constraints across planes of motion. *Experimental Brain Research* 1999;128(1–2):250–255.
- Serrien DJ, Brown P. The functional role of inter-hemispheric synchronization in the control of bimanual timing tasks. *Experimental Brain Research* 2002;147:268–272.
- Sternad D, Dean WJ, Schaal S. Interaction of rhythmic and discrete pattern generators in single-joint movements. *Human Movement Science* 2000;19:627–664.
- Stucchi N, Viviani P. Cerebral dominance and asynchrony between bimanual two-dimensional movements. *Journal of Experimental Psychology: Human Perception and Performance* 1993;19:1200–1220. [PubMed: 8294888]
- Swinnen SP. Intermanual coordination: From behavioural principles to neural-network interactions. *Nature Reviews Neuroscience* 2002;3:348–359.
- Swinnen SP, Jardin K, Meulenbroek R. Between-limb asynchronies during bimanual coordination: Effects of manual dominance and attentional cueing. *Neuropsychologia* 1996;34:1203–1213. [PubMed: 8951832]
- Swinnen SP, Jardin K, Verschueren S, Meulenbroek R, Franz L, Dounskaia N, et al. Egocentric and allocentric constraints in the expression of patterns of interlimb coordination. *Journal of Cognitive Neurosciences* 1997;9:348–377.
- Swinnen SP, Jardin K, Verschueren S, Meulenbroek R, Franz L, Dounskaia N, et al. Exploring interlimb constraints during bimanual graphic performance: Effects of muscle grouping and direction. *Behavior Brain Research* 1998;90:79–87.
- Swinnen SP, Wenderoth N. Two hands, one brain: Cognitive neuroscience of bimanual skill. *Trends in Cognitive Sciences* 2004;8:18–25. [PubMed: 14697399]
- Tseng Y, Scholz JP, Schöner G. Goal-equivalent joint coordination in pointing: Effect of vision and arm dominance. *Motor Control* 2002;6:183–207. [PubMed: 12122226]
- Tseng Y, Scholz JP, Schöner G, Hotchkiss L. Effect of accuracy constraint on joint coordination during pointing movements. *Experimental Brain Research* 2003;149:276–288.
- Tseng YW, Scholz JP. Unilateral vs. bilateral coordination of circle-drawing tasks. *Acta Psychologica (Amsterdam)* 2005;120:172–198.
- Ullen F, Forssberg H, Ehrsson HH. Neural networks for the coordination of the hands in time. *Journal of Neurophysiology* 2003;89:1126–1135. [PubMed: 12574485]

- van Mourik AM, Beek PJ. Discrete and cyclical movements: Unified dynamics or separate control? *Acta Psychologica* 2004;117:121–138. [PubMed: 15464010]
- Walters MR, Carson RG. A method for calculating the circularity of movement trajectories. *Journal of Motor Behavior* 1997;29:72–84.
- Winter, DA. *Biomechanics of human movement*. Wiley; New York: 1979.
- Wuyts IJ, Summers JJ, Carson RG, Byblow WD, Semjen A. Attention as a mediating variable in the dynamics of bimanual coordination. *Human Movement Science* 1996;15:877–897.
- Yang JF, Scholz JP. Learning a throwing task is associated with differential changes in the use of motor abundance. *Experimental Brain Research* 2005;163:137–158.

FIGURE 1.

Illustration of the experimental setup. (A) View from the right side and (B) view from the top for symmetric drawing. The black square at the bottom of each circle (six o'clock position) denotes the starting position of each hand. (C) View from the top for asymmetric drawing. See text for details.

FIGURE 2.

(A) Illustration of joint angle definitions for the right arm (similar definitions apply for the left arm). (B) Schematic example of three-joint redundant configurations, J_i , where $i = \{1, 2, 3, 4, \text{ and } 5\}$, consistent with two different planar hand positions (H_1 and H_2). (C) Different manifolds (UCMs; see text) of the joint configurations associated with each hand position. Variations of joint configurations described by J_1, J_2 , and J_3 (solid lines are goal-equivalent with respect to hand position H_1 but are non-goal-equivalent with respect to hand position H_2 or with respect to subspaces that represent other hand positions (i.e., other UCMs).

FIGURE 3.

Hand paths during symmetric and asymmetric drawing at 1.0- and 2.5-Hz frequency steps obtained while 1 representative participant followed a visual template.

FIGURE 4.

The effect of arm and movement pattern on relative hand path variability over each frequency level, collapsed across template and no-template conditions. Averaged results across participants are shown. CV = coefficient of variation. Error bars show standard errors.

FIGURE 5.

The effect of template and movement pattern on the distance and direction variability (*SD*) of the relative distance between two hands over each frequency level. Averaged results across participants are shown. Error bars show standard errors of the mean *SD*.

FIGURE 6.

The effect of arm and pattern on joint configuration variance underlying control of the individual hand paths over each frequency level. Averaged results across participants are shown. Error bars show standard errors of the mean. *GEV* = goal-equivalent variance. *NGEV* = non-goal equivalent variance. *df* = degree of freedom.

FIGURE 7.

The effect of template and movement pattern on joint configuration variance underlying control of the relative position between two hands over each frequency level. Averaged results across participants are shown. Error bars show standard errors of the mean. df = degree of freedom. *GEV* = goal-equivalent variance. *NGEV* = non-goal-equivalent variance.

FIGURE 8.

A representative example of the net, interaction, and muscle moments (*NM*, *IM*, and *MM*, respectively) extracted for each joint during a fragment of the dominant arm's motion (1.5 Hz). Positive values indicate extension, whereas negative values indicate flexion.

FIGURE 9.

Mean percentage of cycle period for (A) shoulder and (B) elbow joints during which muscle and net moments shared the same sign.

FIGURE 10.

Mean muscle (A) and interaction (B) torque impulses for the elbow joint over each frequency level. Arm and movement pattern are indicated in figure legend. Averaged results across participants are shown. Error bars show standard errors of the mean.

FIGURE 11.

Coefficient of variation (CV) of the nondominant hand's path plotted against the standard deviation (SD) of the elbow's interaction moment (IM) impulse for all movement frequencies. Movement patterns are indicated by different symbols. The dashed line shows the line of best fit. Symm = symmetrical. Asym = asymmetrical.

TABLE 1
Mean $\pm$ Standard Error (*SE*) for Cycle Period Deviation (ms), Circle Size (cm), and Circularity

Variable	Period deviation		Circle size		Circularity	
	<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>
Arm						
Nondominant	21.1	5.0 [*]			0.71	0.03 ^{**}
Dominant	18.9	4.6			0.86	0.01
Template			<i>ns</i>			
Template	32.1	7.6 ^{**}			0.78	0.02 [*]
No template	7.9	3.5	<i>ns</i>		0.80	0.02
Pattern						
Symmetric	11.6	3.7 [*]			0.82	0.02 ^{**}
Asymmetric	28.4	6.9	<i>ns</i>		0.76	0.02
Frequency (Hz)						
1.0	-61.8	15.8 ^{***}	27.5	0.9 ^{***}	0.85	0.02 ^{***}
1.5	-1.9	2.9	26.5	0.8	0.80	0.02
2.0	42.5	13.1	25.8	1.1	0.76	0.02
2.5	101.1	16.6	25.3	1.2	0.74	0.02

Note. *ns* = nonsignificant.

^{*} $p < .05$.

^{**} $p < .01$.

^{***} $p < .001$.