**Title:** Handedness results from Complementary Hemispheric Dominance, not Global Hemispheric Dominance: Evidence from Mechanically Coupled Bilateral Movements.

**Author List:** Elizabeth J. Woytowicz (1),Kelly P. Westlake (1),Jill Whitall (1,2), Robert L. Sainburg (3,4)

**Affiliations:**

(1) Department of Physical Therapy and Rehabilitation Science, University of Maryland School of Medicine, Baltimore, MD

(2) Department of Health Sciences, University of Southhampton, Hampshire, UK

(3) Department of Kinesiology, Penn State University, University Park, PA

(4) Department of Neurology, Penn State Milton S. Hershey Medical Center and College of Medicine, Hershey, PA

**Running Head:** Complementary hemispheric dominance of bilateral movements

**Corresponding author:**

Elizabeth Woytowicz

Department of Neurology

University of California, Irvine

843 Health Sciences Rd

Hewitt Hall 1331

Irvine, CA

Tel: +1-949-824-6032

Fax: +1-949-824-5488

elizabeth.woytowicz@gmail.com

##

## **Abstract**

Two contrasting views of handedness can be described as 1) complementary dominance, in which each hemisphere is specialized for different aspects of motor control, and 2) global dominance, in which the hemisphere contralateral to the dominant arm is specialized for all aspects of motor control. The present study sought to determine which motor lateralization hypothesis best predicts motor performance during common bilateral task of stabilizing an object (e.g. bread) with one hand while applying forces to the object (e.g. slicing) using the other hand. We designed an experimental equivalent of this task, performed in a virtual environment with the unseen arms supported by frictionless air-sleds. The hands were connected by a spring, and the task was to maintain the position of one hand, while moving the other hand to a target. Thus, the reaching hand was required to take account of the spring load to make smooth and accurate trajectories, while the stabilizer hand was required to impede the spring load to keep a constant position. Right-handed subjects performed two task sessions (right hand reach and left hand stabilize; left hand reach and right hand stabilize) with the order of the sessions counterbalanced between groups. Our results indicate a hand by task-component interaction, such that the right hand showed straighter reaching performance while the left showed more stable holding performance. These findings provide support for the complementary dominance hypothesis and suggest that the specializations of each cerebral hemisphere for impedance and dynamic control mechanisms are expressed during bilateral interactive tasks.

**New & Noteworthy**

In this paper, we provide evidence for interlimb differences in bilateral coordination of reaching and stabilizing functions, demonstrating an advantage for the dominant and non-dominant arms for distinct features of control. These results provide the first evidence for complementary specializations of each limb-hemisphere system for different aspects of control within the context of a complementary bilateral task.

**Keywords**

bilateral coordination, lateralization, motor control, handedness

**Introduction**

The lateralized function of the arms and hands has been investigated for more than a century (Elliott & Roy, 1996; McManus, 1985; Sainburg & Kalakanis, 2000; Wang & Sainburg, 2007; Woodworth, 1899). While asymmetries in neural structure and functional activation have been well established and linked to behavioral performance asymmetries (Chen, Cohen, & Hallett, 1997; Chen, Gerloff, Hallett, & Cohen, 1997; Dassonville, Zhu, Ugurbil, Kim, & Ashe, 1997; Haaland & Harrington, 1989a, 1989b, 1994; Kawashima et al., 1993; Kawashima, Inoue, Sato, & Fukuda, 1997; Kawashima, Roland, & O’Sullivan, 1994; Kutas & Donchin, 1974; Macdonell et al., 1991; Viviani, Perani, Grassi, Bettinardi, & Fazio, 1998; Volkmann, Schnitzler, Witte, & Freund, 1998; Winstein & Pohl, 1995; York Haaland & Delaney, 1981), there has been little agreement about the control mechanisms that lead to manual asymmetries (Carson, 1993). There are currently two prominent views of handedness in the literature. One of these hypotheses, referred to as the complementary-dominance hypothesis, posits that each hemisphere is specialized for different aspects of control. A recent example of this view of handedness is the dynamic dominance model, which proposes that the hemisphere contralateral to the dominant (right) arm is specialized for predictive control of dynamics, allowing smooth and efficient coordination of movements, while the hemisphere contralateral to the non-dominant (left) arm is specialized for impedance control that allows for positional stability in the face of unanticipated perturbations (Sainburg, 2005). This hypothesis has been supported by studies of unilateral reaching in both healthy young and older participants (Mutha, Haaland, & Sainburg, 2013; Przybyla, Haaland, Bagesteiro, & Sainburg, 2011; Vivek Yadav & Sainburg, 2014), as well as left-hand dominant individuals (Przybyla, Good, & Sainburg, 2012), and patients with specific cortical lesions (Mani et al., 2013; Schaefer, Haaland, & Sainburg, 2009; Winstein & Pohl, 1995). Alternatively, possibly the most universal and long-standing view of handedness is that the dominant arm is specialized for all aspects of control, while the non-dominant arm is inferior for all aspects of control (Amunts et al., 1996; Liepmann, 1925; Sperry, 1966; Taylor & Heilman, 1980; Volkmann et al., 1998; Ziemann & Hallett, 2001). We refer to this hypothesis as the global dominance hypothesis. In addition to superior performance of skilled movements of the dominant arm, the global dominance hypothesis has also been supported through greater cortical representations and more effective inhibitory interhemispheric control of the left motor cortex in right handers (Volkmann et al., 1998; Ziemann & Hallett, 2001).

Although substantial research has examined these hypotheses by comparing unilateral dominant and non-dominant reaching performance, (for reviews, see Grouios 2006; Sainburg 2014; Serrien, Cassidy, and Brown 2003), less has been directed towards bilateral movements. Since most functional daily activities involve the coordinated use of both arms (Bailey, Klaesner, & Lang, 2015; Kilbreath & Heard, 2005), studies of bilateral tasks can provide additional insights of arm specialization beyond what can be gleaned from unilateral tasks alone. In an investigation of bilateral reaching movements, requiring symmetrical movements with asymmetric force demands, the non-dominant arm demonstrated greater adaptability to dynamic force perturbations induced by dominant arm actions, than vice versa (Yokoi, Hirashima, & Nozaki, 2014). This result suggests that the supporting role of the non-dominant arm results from a different specialization, not an overall inferior level of control, which is consistent with the complementary-dominance hypothesis. Alternatively, phase transitions from the anti-phase to in-phase bilateral movements typically seen with increased movement frequency have been associated primarily with the non-dominant hand and arm (Byblow, Bysouth-Young, Summers, & Carson, 1998; Byblow, Carson, & Goodman, 1994; Byblow, Lewis, Stinear, Austin, & Lynch, 2000; Garry & Franks, 2000; Rogers, Bradshaw, Cunnington, & Phillips, 1998; Semjen, Summers, & Cattaert, 1995; Sherwood, 1994; Treffner & Turvey, 1995; Walter & Swinnen, 1990b). These findings suggest a bilateral coordination deficit in the nondominant, but not the dominant arm and have led some to posit that the left hemisphere is dominant for all aspects of bimanual coordination (Serrien et al., 2003), an idea consistent with the global dominance hypothesis.

The arm-hemisphere specializations of the dynamic dominance model have been suggested to reflect the reaching and stabilizing complementary roles observed during bimanual coordination of the right (dominant) arm and left (non-dominant) arm, respectively (Guiard, 1987; Johansson et al., 2006; Sainburg, Good, & Przybyla, 2013). However, comparisons of reaching performance in the above-mentioned unilateral and bilateral tasks likely provided biased results given that both hypotheses suggest that the dominant (right) arm is specialized for reaching. Further, support for right hemisphere specialization of stabilization has been inferred through greater final position accuracy and impedance control during these tasks. As such, the context of unilateral tasks or rhythmic and symmetrical bilateral tasks do not directly test the right hemisphere specialization aspect of these opposing hypotheses.

While many studies have examined bilateral coordination during rhythmic and symmetrical activities of the arms, a more natural context of bilateral movements is that in which one arm stabilizes against the forces imposed by the activity of the other hand. Everyday examples of this type of behavior include holding nails with one hand, while hammering with the other, opening a jar lid with one hand while stabilizing the jar with the other hand, holding a carrot with one hand and peeling away from body, and holding a loaf of bread with one hand, while slicing with the other. In such tasks, the non-dominant arm tends to stabilize an object against forces imposed by the other hand. Despite the ecological significance of these types of tasks, no investigations have investigated the effect of hemispheric specializations during bilateral coordination of reaching and stabilizing functions with the hands mechanically coupled. The objective of the present study was to investigate which view of handedness best predicts the coordination of both arms during a bilateral task that reflects the coordination required for everyday activities. We developed a novel bilateral coordination paradigm in which one arm maintains a spatial position while the other arm performs a center-out reaching task with a spring affixed between the arms. The stabilizing hand is required to impede the changing spring forces to maintain a constant position while the reaching hand is required to account for the spring forces in order to make smooth and accurate trajectories. In our loaf of bread analogy, the forces imposed on the stabilizing arm reflect both the normal and shearing forces applied by the knife to the bread and vary with the orientation and velocity of the knife. Our task was designed to reflect the time and movement dependent nature of these more natural bimanual tasks. The dynamic dominance hypothesis predicts that the dominant arm should show specialization for reaching against the load, while the non-dominant arm should demonstrate specialization for stabilization. Alternatively, the global dominance hypothesis predicts that the dominant arm will be superior for both aspects of performance.

## **Methods**

### *Participants*

Twenty right-handed young adults, aged 21-35 years (mean = 27.4 ± 2.8 years; 10 males and 10 females), participated in this study. The 13-item Edinburgh Handedness Inventory (EHI) (Oldfield, 1971) was used to confirm that all participants were right-hand dominant (i.e. laterality quotient of 80 or greater). Exclusion criteria included neurological conditions such as stroke, Parkinson's disease, multiple sclerosis; significant musculoskeletal impairments including any upper extremity bone fractures occurring within the past 5 years, and/or soft tissue injuries that would affect performance of the motor task. In addition, musicians, defined as anyone who currently or previously played a musical instrument regularly (>1 hour/week) for an extended period of time (>1 year), were excluded given that musicians have been shown to have more symmetric distal hand motor skills and motor performance (Christman, 1993; Fujii, Kudo, Ohtsuki, & Oda, 2010; Waldron & Anton, 1995), reduced lateralization of attention (Patston, Hogg, & Tippett, 2007), and reduced functional and structural asymmetry of sensorimotor areas between hemispheres (Amunts et al., 1997; Gaser & Schlaug, 2003; Meister et al., 2005; Parsons, 2001). All participants gave written informed consent prior to testing and were paid for their participation. The Institutional Review Board the University of Maryland School of Medicine and the Institutional Review Board of the Penn State College of Medicine prospectively approved all experimental procedures. While all data were collected at the Maryland School of Medicine, de-identified data was shared between sites for analysis.

###

### *Experimental setup.*

The testing paradigm was implemented using KineReachTM, a custom virtual-reality motion tracking system developed at Penn State by R. Sainburg. Both arms were supported on air cushion sleds by continuous pressurized airflow to support the arms on the table-top with negligible friction. The task was reflected from an inverted 60” TV screen by a mirror, which occluded the view of the arms during movement. All joints distal to the elbow were immobilized using an adjustable brace. Trunk movements were restricted using a chest restraint, however, any inadvertent motion of the trunk and scapula was recorded as motion of the proximal upper arm. Position and orientation of the hand-forearm segment and upper arm segment were recorded using two 6- degree of freedom (DOF) magnetic sensors on each arm (Trackstar: Ascension Technology, USA).

###

### *Experimental Task.*

Figure 1 shows the experimental set-up. All participants completed the following two task conditions: (1) right hand reaching and left hand stabilizing, and (2) left hand reaching and right hand stabilizing, with the order of these tasks counterbalanced between participants. The task was performed with a spring attached at both ends to each of the arm sleds. Each of the sessions required ten testing blocks of seven trials with one trial to each target in random order. Both the left and right hand cursors (d = 0.015m) were displaced 0.127 meters medially from the corresponding hand. This medial (relative to the hands) displacement of the cursors on the screen, assured that the cursors could overlap without the hands touching one another. Prior to each trial, a small stretch of the spring was required to bring both cursors into the start circle. This produced spring torques of approximately 1 and 4 Newton-Meters (Nm) at the elbow and shoulder joints, respectively. To begin each trial, both hand cursors were required to stay within the start circle (d = 0.03m) for 300 milliseconds. Each of the seven target circles (d = 0.03m) were arranged radially 0.2m from the start circle. Figure 1 illustrates the experimental task. Figure 1A illustrates the target display seen on the screen, with the actual location of the hands displayed in Figure 1C and 1D, and an example of condition 1 is displayed in Figure 1B.

Figure 1. Experimental Task Setup

Participants were asked to reach to each circle at a minimum peak speed of 0.5 m/s, as accurately as possible. Velocity feedback was provided in the form of a thermometer-style display and if movements did not meet the 0.5 m/s threshold, participants did not receive points for accuracy. Participants were instructed to aim for the center of the target and prior to the reach, a smaller target circle was displayed within the center of the target circle to reinforce this instruction. Once the cursor left the start circle, this smaller center circle was removed from the target circle. During the reach, the other hand was required to stay within the start circle, requiring participants to stabilize against the increasing spring load. Participants were able to monitor the position of each hand as a cursor during the movement, and were able to view the completed hand-path as a series of small circles, reflecting the position of each hand drawn every 32 milliseconds, following each trial. After each trial, participants were awarded points based on how close they reached to the center of the target.

###

### *Data processing and analysis.*

All kinematic, kinetic, and dynamic analyses were processed with custom programs written in IgorPro (version 6.37, WaveMetrics). The data were low-pass filtered at 8 Hz with a third order dual-pass Butterworth filter before differentiation to obtain velocity and acceleration profiles. Movement onset and offset were defined using the reaching arm. The start of each reach was defined as the first minimum in tangential velocity that was under 8% of the maximum velocity for that trial. The end of each reach was defined as the first minimum following peak velocity that was below 8% of maximum velocity. Then, movement onset and offset of the stabilizing hand was defined using these reaching movement times.

###

### *Kinematic analysis.*

To compare reaching arm performance, kinematic analyses included calculation of deviation from linearity and final position error. Hand path deviation from linearity was defined as the minor axis of the path divided by the major axis of the path. The major axis was defined as the longest distance between any two points parallel to the hand path, and the minor axis was defined as the longest distance between any two points perpendicular to the major axis. Final position error was calculated as the Euclidean distance between the cursor center (index of fingertip) at the end of the reach and the target center. Lower values of both deviation from linearity and final position error are indicative of straighter trajectories and more accurate final positions.To compare stabilizing arm performance, we calculated mean hand displacement and maximum acceleration. Given that the goal of the stabilizing arm is to remain stationary, lower values of both variables indicate more stable performance.

###

### *Inverse Dynamics*

The terms in the equations of motion were partitioned into four main components to calculate 1) muscle torque, which estimates the rotational forces from muscle contraction; 2) interaction torque, representing forces imposed by the movement of other limb segments; 3) net torque, the sum of the muscle and interaction torques (Bagesteiro & Sainburg, 2003), and 4) Spring torque (see figure 2). Interaction torque generated at the elbow resulted from shoulder linear and rotational accelerations and velocities. Any motion of the trunk was reflected by our measure of shoulder point acceleration, and thus is included in our interaction torque term. Limb segment inertia, center of mass location, and mass were computed using each participant’s body weight and limb segment lengths (Winter, 1990).

Figure 2 shows a schematic to demonstrate the configuration of the spring (left), and the vectors representing the forces associated with this configuration (middle). It should be noted that the actual amplitude of the forces will vary with the distance between the connection on the left and right hand supports minus the slack distance of the spring: Fspring = Kspring(dlr – d slack), where Fspring = 0 when (dlr – d slack) < 0. The right side of figure 2 shows the spring force for one arm separately, as used to calculate the inverse dynamics for that arm, as detailed below.

Figure 2. Schematic of Spring Forces

*Elbow joint torques*

Tel=meresin(θs+θe)x¨−merecos(θs+θe)y¨−lsmeresin(θe)θ˙2s

−(Ie+mere[re+lscos(θe)])θ¨s

TeN=(Ie+mer2e)θ¨e

Te spring = – [le sin(θe + θs)] Fx + [le cos(θe + θs)] Fy

TeM=TeN−Tel−Te spring

*Shoulder joint torques*

Tsl=(msrssin(θs)+melssin(θs))x¨−(msrscos(θs)+melscos(θs))y¨−(mere(lecos(θe)θ¨e+lssin(θe)θ˙2e+2lssin(θe)θ˙sθ˙e+lssin(θe)θ˙2s))

TsN=(Is+msr2s+mel2s+melsrecos(θe))θ¨s

Ts spring = [(lssin(θs) – le sin(θe + θs)] Fx + [(lscos(θs) – le cos(θe + θs)] Fy

TsM=TsN−Tsl+TeM−Ts spring

where *m* is mass of segment, *r* is center of mass of segment, *l* is length of segment, *I* is inertia of segment, θs is shoulder angle, θe is angle between center of mass of lower arm segment and upper arm, *x* is shoulder position along *x* direction, *y* is shoulder position along *y* direction, *Te* I is elbow interaction torque, *Te* M is elbow muscle torque, *Te* N is elbow net torque, *Te* spring is elbow spring torque, *Ts* I is shoulder interaction torque, *Ts* M is shoulder muscle torque, and *Ts* N is shoulder net torque, *Ts* spring is shoulder spring torque. The subscripts are defined as follows: s is upper arm segment and e is lower arm segment (including support and air sled device).

### *Mechanical Compliance*

We computed endpoint and joint compliance for the stabilizing arm. Accurate performance should have stabilized the hand against the spring forces, requiring high-stiffness and low compliance. Therefore, greater compliance indicated a greater tendency to move when the spring force was applied, i.e. worse stabilizing performance. Compliance was estimated at the hand and computed at each joint. As an estimate of endpoint compliance, total hand displacement was divided by the peak spring force. At the elbow and shoulder, joint compliance was calculated as the slope of the relationship between joint position and spring torque across a trial (i.e. joint displacement relative to change in spring torque).

Hand Compliance = s/ Fspring (peak) , where s = cumulative distance moved within the trial

Joint Compliance shoulder = Slope of regression between joint position (θs) and Ts spring

Joint Compliance elbow = Slope of regression between joint position (θe) and Te spring

### *Statistical Analysis*

To ensure participants were familiarized with the task and to control for any potential effects of interlimb transfer, we limited all analyses to steady-state performance. To ensure that we were including only participants’ steady-state performance, we calculated the mean coefficient of variation (CV) for peak velocity and end error of all testing sessions (Sainburg, Schaefer, & Yadav, 2016). Measures of CV were used to assess the block in which the CV of both arms appeared to reach an asymptote. We then used an ANOVA to assure that for the remaining blocks, there was not a main effect of block on CV, thus verifying steady-state performance. We statistically assessed steady-state performance by a 2 (arm) by 10 (block) by 2 (task condition) mixed factor ANOVA of peak velocity CV and a 2 (arm) by 10 (block) mixed factor ANOVA of end error CV. The first blocks with highest CV were then excluded, steady-state performance was confirmed with a subsequent mixed factor ANOVA including only the remaining blocks, and dependent variables were then collapsed across these remaining blocks for further analysis. Exclusion of data from both arms (vs. comparing performance within each arm) was performed to ensure main comparisons of interest between arms were based off of average performance of comparable blocks.

Further, given the relationship between movement velocity and accuracy (Fitt, 1954), prior to testing our primary hypothesis, we needed to first ensure that peak movement velocity of the reaching arm was comparable for both arms. To do so, we performed a mixed factor ANOVA on mean peak velocity data with arm and target as within-subject factors. We expected only a main effect of target direction, but no effect of arm, thereby indicating comparable left and right reaching arm peak velocities.

In addition, as endpoint stiffness varies based on arm orientation and force direction (Perreault, Kirsch, & Crago, 2002) we grouped the trials with reaching targets located medial, center, and lateral with respect to the start position of the reaching arm, as indicated in Figure 1C and 1D. Therefore, to compare reaching and stabilizing performance, repeated-measure mixed model ANOVAs with within-group factors of arm (right, left) and target clusters (medial, center, lateral were used. The alpha value for our ANOVAs and post-hoc tests was set to 0.05, and all data are reported in the format of mean ± standard error. Bonferroni correction method was used during post hoc comparisons. All statistical analyses were completed using JMP software (SAS Institute Inc., Cary, NC).

## **Results**

### *Steady-state Performance*

We first identified steady state performance. For this analysis, we averaged across each 7 trial increment, which included a single movement to each target. This resulted in 10 separate blocks, together totaling all 70 trials. We then used our measures of CV to assess the block in which the CV appeared to reach an asymptote. Peak velocity CV appeared consistent and was confirmed with no significant main effect of block [F(9,324) = 1.61, p = 0.2331]. However, final position error did not appear to reach an asymptote for both hands until after block 2 (Figure 3). After removing the data from blocks 1 and 2 from the analysis, we ran a second one-way ANOVA for block X arm, which revealed no significant main effect of block [F(7,126) = 0.37, p = 0.9179]. We therefore, restricted our steady state results to data from blocks 3-10.

Figure 3. Steady State Performance.

### Figure 4. Example Kinematics and Dynamics.

Figure 4A shows representative arm movements for both task conditions, reach and stabilize. Each shoulder, elbow, wrist and finger path is shown, with stick figures representing the upper arm, forearm, and hand, drawn every 2 points (~16 milliseconds). In the left column, the left arm reached toward the target, while the right arm stabilized against the imposed spring load, while in the right column, the right arm reached and left arm stabilized. In both movements, the reaching arm show grossly similar kinematics, for these examples. The orientation and length of the spring is shown at the start (dashed) and end (solid) of each movement. Notice that both the orientation of the spring and the length of the spring change during the reach. Figure 4B illustrate the hand path of the stabilizing arms (magnified in scale compared to Figure 4A) illustrating greater displacement of the right stabilizing arm compared to the left stabilizing arm. Figure 4C and 4D show the joint torque components at the elbow and shoulder respectively in the stabilizing arm. The spring torque (thick gray), muscle torque (thick black), and net torque (thin black) are all shown. Because the net torque reflects the product of the acceleration of the joint and the segments’ effective inertia, a zero value indicates stability. Notice that the net torque for the right stabilizing arm shows higher variation about zero than does the net torque for the left stabilizing arm.

 Analysis of the coordination between the spring and muscle torques demonstrates the origin of these differences in stability. At both joints, the spring torque at the beginning of the trial is roughly 1 Nm at the elbow and roughly 4 Nm at the shoulder. This results from the elongation of the spring required to place both cursors in the start circle. As the reaching hand moves toward the target, the angle between the spring and forearm becomes smaller, resulting in a reduction in elbow spring torque. However, the angle between the spring and the upper arm becomes larger throughout the movement as does the length of the spring, both factors combining to increase in spring torque at the shoulder. The muscle torque at both joints for each arm counters the changes in spring torque. However, for the left arm, the muscle torque closely mirror images the spring torque, maintaining a near zero net torque at both joints. For the right arm, the muscle torque shows variations that do not mirror the spring torque, resulting in net torque variations. Thus, the left arm effectively impedes the forces generated by the moving spring, while the right does so less effectively. We will next present the statistical analyses of these data, across trials and participants.

### *Reaching Kinematics*

Our 2-way ANOVA (Target X Arm) indicated that while peak velocity of the reaching arm varied with target cluster [F(2,38) = 179.88, p < 0.0001], it did not vary between the arms [F(1,19) = 0.02, p = 0.8789]. In addition, we found no significant interactions [F(2,38) = 2.34, p = 0.1101].

While both arms showed grossly similar reaching kinematics in the representative example illustrated, analysis of hand path linearity and final position error showed significant differences between the arms. As shown in Figure 5, which shows mean deviation from linearity and final position error for both arms, across the 3 target clusters, the right arm demonstrated superior reaching performance, with less deviation from linearity and end error compared to the left arm. Our 2-way ANOVA (Target X Arm) revealed a main effect for hand, with significantly greater deviation from linearity for the left hand-paths [F(1,19) = 32.66, p < 0.0001]. Deviation from linearity also varied significantly with target cluster [F(2,38) = 29.91 p < 0.0001] with a significant hand by target interaction [F(2,38) = 3.46, p = 0.0417]. Figure 5 (right column) shows that final position error varied between the arms [F(1,19) = 19.42, p = 0.0003], but not between target clusters [F(2,38) = 1.98 p = 0.1522]. There were no significant hand by target interactions [F(2,38) = 0.95 p = 0.3946].

Figure 5. Reaching: Kinematic Interlimb Differences

Figure 6. Stabilizing: Kinematic Interlimb Differences

###

### *Stabilizing Arm*

As illustrated by the examples in figure 4, the right stabilizing arm showed greater displacement than the left stabilizing arm. Figure 6 (left) shows the mean hand displacement for the stabilizing arm across all 3 target clusters. When stabilizing against the spring force, the right arm moved significantly more than the left arm, as revealed by a main effect of arm in our 3-way ANOVA [F(1,19) = 6.05, p = 0.0237] and both arms moved more when the reaching target was located more medially, as revealed by a main effect of target cluster [F(2,38) = 63.96, p < 0.0001]. We found no significant interaction between target and hand [F(2,38) = 0.12, p = 0.8878]. Because of the differences in reaching kinematics between the arms described above, we next asked whether the spring forces experienced between the arms might have been significantly different. Figure 6 (right) shows the maximum spring forces for each target cluster and for each hand. Our 2-way ANOVA revealed a main effect for target cluster [F(2,38) = 3080.18, p < 0.0001] as expected by the differences in geometry for the different target directions, but no significant main effects for hand, [F(1,19) = 1.21, p = 0.2846], indicating that both arms experienced similar spring forces, reflected also by no interaction between hand and target cluster [F(2,38) = 1.21, p = 0.3098].

The differences between hands in maintaining a stable position in the face of similar spring forces suggested a difference in compliance between the hands. We, therefore quantified compliance at the hand (end-point compliance) and at each joint (see methods). As shown in figure 7A, endpoint compliance varied with target cluster [F(2,38) = 92.83, p < 0.0001], was significantly greater for the right arm [F(1,19) = 6.61, p = 0.0187], and there was no significant interaction between target and hand [F(2,38) = 0.14, p = 0.8742]. Our measures of joint compliance are shown in figure 7B (elbow compliance) and figure 7C (shoulder compliance). Again, joint compliance varied across targets, and the right elbow was more compliant. Our 2-way ANOVA showed a main effect for target [F(2,38) = 23.81, p < 0.0001], and for arm [F(1,19) = 8.58, p = 0.0086], and no significant interaction between target and hand [F(2,38) = 1.34, p = 0.2732]. Compliance at the shoulder also varied with target [F(2,38) = 14.83, p < 0.0001], but was not significantly different between the arms [F(1,19) = 0.00, p = 0.9500], and no significant interaction between target and hand [F(2,38) = 1.44, p = 0.2504]. Thus, the greater compliance of the right arm appears to occur primarily due to differences at the elbow.

Figure 7. Stabilizing Arm Compliance

Overall, our results demonstrate an advantage in accuracy and linearity for the right reaching arm, and in stability for the left-stabilizing arm within the context of a complementary bilateral task..

## **Discussion**

The current study investigated whether handedness is best described by a complementary-dominance or global-dominance hypothesis of arm-hemisphere specializations. We assessed participant’s performance on bilateral coordination tasks that require stabilization of one hand against forces imposed by the actions of the other hand. Two groups of young, right hand dominant, adults completed the bilateral coordination paradigm in which one arm maintained its spatial position and the other arm performed a center-out reaching task with a spring affixed between the arms. The dynamic dominance hypothesis, a case of complementary-dominance, predicted that the dominant arm would demonstrate superior reaching performance against the load, while the non-dominant arm would show superior performance for stabilizing against the load. The global-dominance hypothesis predicted that the dominant arm would demonstrate superior performance for both reaching and stabilizing. Our results illustrated better kinematic performance of the right dominant arm for reaching, and better performance of the left non-dominant arm for stabilizing. The left arm muscle torques more effectively countered imposing spring torques to stabilize the arm, as reflected by lower compliance at the joints and at the hand. Thus, our results provide support for complementary specializations of each limb-hemisphere system for different aspects of control, rather than global specialization of the dominant limb-hemisphere for all aspects of control.

### *Hemispheric specialization for Reaching and Coordinating Intersegmental Dynamics*

Our findings are consistent with previous studies of unilateral reaching in right-handers that proposed a left hemisphere specialization for predictive mechanisms that can specify efficient and smooth trajectories under stable environmental conditions (Mutha et al., 2013; Wang & Sainburg, 2007), and extend these findings to include bilateral movements. During unilateral reaching movements made in the horizontal plane, (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis, 2000), when dominant and non-dominant arm movements were matched for speed, the dominant arm trajectories were substantially straighter, and were produced with lower muscle torque and lower normalized electromyographic activity and mean squared torque across the shoulder and elbow joints (Bagesteiro and Sainburg, 2002). In these studies, the more torque-efficient movements of the dominant arm were associated with more efficient coordination of muscle torques with intersegmental interaction torques. Such dominant arm advantages in intersegmental coordination were later extended to both vertical reaching movements (Tomlinson and Sainburg 2012) and horizontal plane reaching movements (Schaffer and Sainburg, 2016) that were performed without arm-support under normal gravitational conditions. Consistent with these findings, Pigeon et al. (Pigeon, Dizio et al. 2013), showed dominant arm advantages in intersegmental coordination during turn-and-reach movements performed while subjects were standing. Coriolis torques were generated on the arm during trunk rotation that were well-compensated by the dominant, but not the non-dominant arm. Similarly, Hore and colleagues reported dominant arm advantages in coordinating intersegmental dynamics during overarm throwing (Hore, Watts et al. 1996, Hore, Watts et al. 1999, Debicki, Gribble et al. 2004, Hore, O'Brien et al. 2005, Debicki, Gribble et al. 2011). Thus, a wide range of research has demonstrated dominant arm specialization for coordinating intersegmental dynamics, a process that relies on feedforward use of vision and proprioception in predictive control processes (Ghez, Gordon et al. 1990, Sainburg, Poizner et al. 1993, Ghez, Gordon et al. 1994, Gordon, Ghilardi et al. 1994, Ghez, Gordon et al. 1995, Ghez and Sainburg 1995). Our current findings, demonstrating dominant arm advantages in reaching coordination that requires compensation of both intersegmental and object interaction (spring) dynamics, are consistent with this line of work and extend this advantage to bilateral movement conditions. Thus, we conclude that specialization of predictive control of limb dynamics for efficient reaching trajectories is expressed during a cooperative bilateral task in which the arms are coupled mechanically but perform different tasks.

### *Hemispheric specialization for Impedance Control*

While specialization of the dominant hemisphere/arm for predictive coordination of reaching and overarm throwing has been well established, the idea that the non-dominant hemisphere/arm might be specialized for some aspects of control has been less well established. Previous studies have, nevertheless, suggested that the non-dominant system might be specialized for impedance control, as required to stabilize against unpredictable environmental forces, or mechanical interactions imposed by motion of the dominant arm during bilateral tasks. In fact, Shabowsky et al (2007) as well as Duff and Sainburg (2007) demonstrated that while both arms adapted with similar efficacy to novel force fields, the dominant arm did so through predictive mechanisms while the non-dominant arm relied on impedance control mechanisms that generated lower amplitude after-effects when the field was suddenly removed. The non-dominant arm also has been shown to more efficaciously control unexpected inertial loading, through both short and long latency proprioceptive reflexes (Bagesteiro & Sainburg, 2003). A more direct test of the hypothesis that the non-dominant arm is specialized for impedance control was recently reported (Vivek Yadav & Sainburg, 2014). In this study, unilateral reaching movements were made in multiple directions, while force fields were applied through a robotic manipulandum. In one case, the field was consistent between trials, and the dominant arm adapted to this field quicker and to a greater extent. In the other case, the field varied in amplitude between trials and was thus unpredictable. The non-dominant arm adapted more quickly and to a greater extent to the unpredictable field than did the dominant arm, demonstrating an advantage of the non-dominant arm under unpredictable mechanical conditions, as expected for an impedance controller. These results are not only consistent with the complementary specializations demonstrated by previous unilateral studies, but also demonstrates the utility of these specializations during a mechanically coupled bilateral task.

*Bihemispheric Control of arm movements*

If each hemisphere is specialized for different aspects of motor control, then lesion of one hemisphere should produce predictable motor deficits in the ipsilesional arm of previously right-hand dominant stroke patients. This bold hypothesis has been supported by reports of ipsilesional motor deficits as early as 1967 (Chestnut & Haaland, 2008; Haaland et al., 2009; Haaland, Prestopnik, Knight, & Lee, 2004; Hermsdörfer, Ulrich, Marquardt, Goldenberg, & Mai, 1999; Sainburg & Duff, 2006; Schaefer, Haaland, & Sainburg, 2007; Schaefer et al., 2009; Swinnen, Debaere, Puttemans, Vangheluwe, & Kiekens, 2002; Wetter, Poole, & Haaland, 2005; Winstein & Pohl, 1995; Wyke, 1967; Yarosh, Hoffman, & Strick, 2004). Furthermore, we proposed that ipsilateral movement deficits following unilateral brain damage should produce different movement deficits in the ipsilesional, non-paretic arm of stroke patients, who were previously right-hand dominant. Left hemisphere damage should produce left arm deficits in intersegmental coordination and trajectory control, while right hemisphere damage should produce right-arm deficits in the ability to accurately stabilize the position of the arm. In fact, numerous studies have supported this hypothesis (Haaland et al., 2004; Mani et al., 2013; Schaefer et al., 2009). According to our complementary dominance model of motor control, the asymmetry in performance associated with handedness in healthy individuals emerges from different specializations of each hemisphere’s motor control system. While previous studies have supported this hypothesis during unilateral movements, our current findings extend these specializations of each hemisphere/arm system during the performance of bilateral movements. These findings, thus, support the complementary dominance hypothesis.

Consistent with the global dominance hypothesis, many previous investigations of bilateral coordination have suggested that the left hemisphere is generally dominant for all aspects of bimanual movement (Byblow et al., 1998, 1994, 2000; Garry & Franks, 2000; Kimura, 1977; Rogers et al., 1998; Semjen et al., 1995; Serrien et al., 2003; Sherwood, 1994; Treffner & Turvey, 1995; Walter & Swinnen, 1990a). However, given our current findings, we suggest that this conclusion may have been confounded by the motor control demands of the tasks performed in these studies. Often, such studies invoke tasks that require rhythmic motions of the arms in predictable mechanical conditions. Thus, it is not surprising that the left hemisphere/right arm (in right-handers) appeared dominant for control of these bilateral tasks. For bilateral tasks requiring mechanical conditions that are not predictable, we might expect different results. For example, the left non-dominant arm might provide a more robust stabilization of the bilateral task against unpredictable perturbations than the right dominant arm. In fact, Schaffer and Sainburg (2017) recently reported that the left-nondominant arm’s response to right arm perturbations in a bilateral task is more robust than that of the right-dominant arm’s response to left arm perturbations. Consistent with this finding, our current results indicate that when performing complementary tasks, each limb is ‘dominant’ for processes that reflect the specialization of its contralateral hemisphere.

### *Asymmetric task demands during bilateral coordination*

Prior investigations of bilateral coordination during symmetric bilateral tasks have described evidence for asymmetric interference between the arms, such that the right (dominant) hand tends to lead the left (non-dominant) hand, with greater error when the left arm is required to lead or perform the more complex task (de Poel, Peper, & Beek, 2007; Stucchi & Viviani, 1993; Treffner & Turvey, 1996; Walter & Swinnen, 1990a; Woytowicz, Whitall, & Westlake, 2016). For example, a previous study demonstrated that during a bilateral force production task, when the dominant hand performed the more complex force task both arms were able to complete different tasks with little interference from the other hand (Hu & Newell, 2011). In contrast, when the non-dominant arm performed the more complex force task, there was greater performance error for each independent task with less movement differences between the hands. This phenomenon, described as asymmetric interference or bilateral “coupling” is thought to reflect cross talk (motor overflow) between the control processes of each arm (Marteniuk & MacKenzie, 1980; Spijkers & Heuer, 1995). Motor overflow has been suggested to occur via callosal pathways from the hand performing the more demanding task (Diedrichsen, Hazeltine, Nurss, & Ivry, 2003). However, our current results suggest that what is ‘demanding’ for one hand may not be demanding for the other hand. Therefore, we now suggest that bilateral coupling or interference might reflect the recruitment of the ipsilateral hemisphere when a task demands a hand to perform a task for which the contralateral hemisphere is not specialized. For example, impedance control for the dominant arm and predictive control of dynamics for the non-dominant arm.

*Limitations*

 Given that the medial displacement of the cursors created a visuo-proprioceptive conflict, it is possible that performance differences could have occurred due to hemispheric differences in responsivity to visuo-proprioceptive conflict, rather than hemispheric specialization for different aspects of motor control. An alternative experimental set-up could have required each hand start in a separate start circle, which accurately represented arm location. While this would have reduced the visuo-proprioceptive conflict demands, this set-up would have increased the attentional demands of the task. Given that prior studies have illustrated lateralization for different aspects of attention (De Schotten et al., 2011) and there has been no evidence to date which suggests there are hemispheric differences in responsivity to visuo-proprioceptive conflict, it was determined the final set-up would best minimize the effect of additional hemispheric specializations. Further, hemispheric responsivity differences would have been illustrated at movement onset, when both hands were required to resolve this conflict to start each trial. However, it is still possible this could have created performance differences throughout the task, which cannot be discounted without further investigation.

 Further, the current results cannot differentiate whether the differences in stabilizing performance occurred because of differences in reactive mechanisms, or differences in predictively compensating for the disturbances imposed by the reaching arm (Bays & Wolpert, 2006; Jackson & Miall, 2008; Yokoi et al., 2014). It is likely that predictive modulation of feedback circuits takes place (Todorov, 2004) and we have previously shown that non-dominant arm specialization for impedance mechanisms occurs largely through predictive modulation of rapid reflex responses to imposed forces (Bagesteiro & Sainburg, 2003; Duff & Sainburg, 2007; V Yadav & Sainburg, 2011). Further research is necessary in order to differentiate the relative contributions of feedforward and feedback mechanisms to the stabilization of the hands in this bilateral task.

 Our previous research has demonstrated through lesion analysis in stroke patients that differences in performance between the dominant and non-dominant arms for different aspects of motor control are related to the specialization of specific regions of the contralateral hemisphere for those processes (Mutha, Sainburg, & Haaland, 2011; Schaefer et al., 2007, 2009; Schaefer, Mutha, Haaland, & Sainburg, 2012). However, it is important to note that our model of hemispheric lateralization is a bilateral model, in which both hemispheres contribute specific processes to each arm, albeit asymmetrically with greatest contribution from the contralateral hemisphere. In the current discussion, we have tended to infer hemispheric specialization based on the performance of the contralateral arm. It should be noted, however, that we cannot conclusively determine whether our current results are due to specific contributions of the right or left hemisphere for reaching or stabilizing. In order to test this hypothesis, further research would be required, using either lesion models or by recording brain activations through fMRI or other methods.

### *Conclusions*

In conclusion, the present study provides evidence for interlimb differences in bilateral coordination of reaching and stabilizing functions, demonstrating an advantage for the dominant and non-dominant arms for these distinct features of control. To date, these results provide the first evidence of the dynamic dominance hypothesis within the context of a complementary bilateral task.

**Grants**

This research was supported by the American College of Sport’s Medicine Doctoral Student Research Award.

**References**

Amunts, K., Schlaug, G., Jäncke, L., Steinmetz, H., Schleicher, A., Dabringhaus, A., & Zilles, K. (1997). Motor cortex and hand motor skills: structural compliance in the human brain. *Human Brain Mapping*, *5*(3), 206–215.

Amunts, K., Schlaug, G., Schleicher, A., Steinmetz, H., Dabringhaus, A., Roland, P. E., & Zilles, K. (1996). Asymmetry in the human motor cortex and handedness. *Neuroimage*, *4*(3), 216–222.

Bagesteiro, L. B., & Sainburg, R. L. (2003). Nondominant Arm Advantages in Load Compensation During Rapid Elbow Joint Movements. *Journal of Neurophysiology*, *90*(3).

Bailey, R. R., Klaesner, J. W., & Lang, C. E. (2015). Quantifying Real-World Upper-Limb Activity in Nondisabled Adults and Adults With Chronic Stroke. *Neurorehabilitation and Neural Repair*, *29*(10), 969–78.

Bays, P. M., & Wolpert, D. M. (2006). Actions and consequences in bimanual interaction are represented in different coordinate systems. *Journal of Neuroscience*, *26*(26), 7121–7126.

Byblow, W. D., Bysouth-Young, D., Summers, J. J., & Carson, R. G. (1998). Performance asymmetries and coupling dynamics in the acquisition of multifrequency bimanual coordination. *Psychological Research*, *61*(1), 56–70.

Byblow, W. D., Carson, R. G., & Goodman, D. (1994). Expressions of asymmetries and anchoring in bimanual coordination. *Human Movement Science*, *13*(1), 3–28.

Byblow, W. D., Lewis, G. N., Stinear, J. W., Austin, N. J., & Lynch, M. (2000). The subdominant hand increases the efficacy of voluntary alterations in bimanual coordination. *Experimental Brain Research*, *131*(3), 366–374.

Chen, R., Cohen, L. G., & Hallett, M. (1997). Role of the ipsilateral motor cortex in voluntary movement. *Canadian Journal of Neurological Sciences*, *24*(4), 284–291.

Chen, R., Gerloff, C., Hallett, M., & Cohen, L. G. (1997). Involvement of the ipsilateral motor cortex in finger movements of different complexities. *Annals of Neurology*, *41*(2), 247–254.

Chestnut, C., & Haaland, K. Y. (2008). Functional significance of ipsilesional motor deficits after unilateral stroke. *Archives of Physical Medicine and Rehabilitation*, *89*(1), 62–68.

Christman, S. (1993). Handedness in musicians: Bimanual constraints on performance. *Brain and Cognition*, *22*(2), 266–272.

Dassonville, P., Zhu, X.-H., Ugurbil, K., Kim, S.-G., & Ashe, J. (1997). Functional activation in motor cortex reflects the direction and the degree of handedness. *Proceedings of the National Academy of Sciences*, *94*(25), 14015–14018.

de Poel, H. J., Peper, C. L. E., & Beek, P. J. (2007). Handedness-related asymmetry in coupling strength in bimanual coordination: furthering theory and evidence. *Acta Psychologica*, *124*(2), 209–237.

De Schotten, M. T., Dell’Acqua, F., Forkel, S. J., Simmons, A., Vergani, F., Murphy, D. G. M., & Catani, M. (2011). A lateralized brain network for visuospatial attention. *Nature Neuroscience*, *14*(10), 1245.

Diedrichsen, J., Hazeltine, E., Nurss, W. K., & Ivry, R. B. (2003). The role of the corpus callosum in the coupling of bimanual isometric force pulses. *Journal of Neurophysiology*, *90*(4), 2409–2418.

Duff, S. V, & Sainburg, R. L. (2007). Lateralization of motor adaptation reveals independence in control of trajectory and steady-state position. *Experimental Brain Research*, *179*(4), 551–561.

Elliott, D., & Roy, E. A. (1996). *Manual Asymmetries in Motor Performance*. CRC Press.

Fitt, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, *47*(6), 381–391.

Fujii, S., Kudo, K., Ohtsuki, T., & Oda, S. (2010). Intrinsic constraint of asymmetry acting as a control parameter on rapid, rhythmic bimanual coordination: a study of professional drummers and nondrummers. *Journal of Neurophysiology*, *104*(4), 2178–2186.

Garry, M. I., & Franks, I. M. (2000). Reaction time differences in spatially constrained bilateral and unilateral movements. *Experimental Brain Research*, *131*(2), 236–243.

Gaser, C., & Schlaug, G. (2003). Brain Structures Differ between Musicians and Non-Musicians. *J. Neurosci.*, *23*(27), 9240–9245.

Grouios, G. (2006). Right hand advantage in visually guided reaching and aiming movements: brief review and comments. *Ergonomics*, *49*(10), 1013–1017.

Guiard, Y. (1987). Asymmetric Division of Labor in Human Skilled Bimanual Action. *Journal of Motor Behavior*.

Haaland, K. Y., & Harrington, D. L. (1989a). Hemispheric control of the initial and corrective components of aiming movements. *Neuropsychologia*, *27*(7), 961–969.

Haaland, K. Y., & Harrington, D. L. (1989b). The role of the hemispheres in closed loop movements. *Brain and Cognition*, *9*(2), 158–180.

Haaland, K. Y., & Harrington, D. L. (1994). Limb-Sequencing Deficits After Left but not Right Hemisphere Damage. *Brain and Cognition*, *24*(1), 104–122.

Haaland, K. Y., Prestopnik, J. L., Knight, R. T., & Lee, R. R. (2004). Hemispheric asymmetries for kinematic and positional aspects of reaching. *Brain*, *127*(5), 1145–1158.

Haaland, K. Y., Schaefer, S. Y., Knight, R. T., Adair, J., Magalhaes, A., Sadek, J., & Sainburg, R. L. (2009). Ipsilesional trajectory control is related to contralesional arm paralysis after left hemisphere damage. *Experimental Brain Research*, *196*(2), 195–204.

Hermsdörfer, J., Ulrich, S., Marquardt, C., Goldenberg, G., & Mai, N. (1999). Prehension with the ipsilesional hand after unilateral brain damage. *Cortex*, *35*(2), 139–161.

Hu, X., & Newell, K. M. (2011). Aging, visual information, and adaptation to task asymmetry in bimanual force coordination. *Journal of Applied Physiology (Bethesda, Md. : 1985)*, *111*(6), 1671–80.

Jackson, C. P. T., & Miall, R. C. (2008). Contralateral manual compensation for velocity-dependent force perturbations. *Experimental Brain Research*, *184*(2), 261–267.

Johansson, R. S., Theorin, A., Westling, G., Andersson, M., Ohki, Y., & Nyberg, L. (2006). How a lateralized brain supports symmetrical bimanual tasks. *PLoS Biology*, *4*(6), e158.

Kawashima, R., Inoue, K., Sato, K., & Fukuda, H. (1997). Functional asymmetry of cortical motor control in left‐handed subjects. *Neuroreport*, *8*(7), 1729–1732.

Kawashima, R., Roland, P. E., & O’Sullivan, B. T. (1994). Activity in the human primary motor cortex related to ipsilateral hand movements. *Brain Research*, *663*(2), 251–256.

Kawashima, R., Yamada, K., Kinomura, S., Yamaguchi, T., Matsui, H., Yoshioka, S., & Fukuda, H. (1993). Regional cerebral blood flow changes of cortical motor areas and prefrontal areas in humans related to ipsilateral and contralateral hand movement. *Brain Research*, *623*(1), 33–40.

Kilbreath, S. L., & Heard, R. C. (2005). Frequency of hand use in healthy older persons. *Australian Journal of Physiotherapy*, *51*(2), 119–122.

Kimura, D. (1977). Acquisition of a motor skill after left-hemisphere damage. *Brain: A Journal of Neurology*, *100*(3), 527–542.

Kutas, M., & Donchin, E. (1974). Studies of squeezing: handedness, responding hand, response force, and asymmetry of readiness potential. *Science*, *186*(4163), 545–548.

Liepmann, H. (1925). Apraktische störungen. *Lehrbuch Der Nervenkrankheiten*, 408–416.

Macdonell, R. A. L., Shapiro, B. E., Chiappa, K. H., Helmers, S. L., Cros, D., Day, B. J., & Shahani, B. T. (1991). Hemispheric threshold differences for motor evoked potentials produced by magnetic coil stimulation. *Neurology*, *41*(9), 1441.

Mani, S., Mutha, P. K., Przybyla, A., Haaland, K. Y., Good, D. C., & Sainburg, R. L. (2013). Contralesional motor deficits after unilateral stroke reflect hemisphere-specific control mechanisms. *Brain*, *136*(4), 1288–1303.

Marteniuk, R. G., & MacKenzie, C. L. (1980). A preliminary theory of two-hand coordinated control. *Tutorials in Motor Behavior*, *1*, 185–197.

McManus, I. C. (1985). Right- and left-hand skill: failure of the right shift model. *British Journal of Psychology (London, England : 1953)*, *76 ( Pt 1)*, 1–34.

Meister, I., Krings, T., Foltys, H., Boroojerdi, B., Müller, M., Töpper, R., & Thron, A. (2005). Effects of long‐term practice and task complexity in musicians and nonmusicians performing simple and complex motor tasks: Implications for cortical motor organization. *Human Brain Mapping*, *25*(3), 345–352.

Mutha, P. K., Haaland, K. Y., & Sainburg, R. L. (2013). Rethinking motor lateralization: specialized but complementary mechanisms for motor control of each arm. *PloS One*, *8*(3), e58582.

Mutha, P. K., Sainburg, R. L., & Haaland, K. Y. (2011). Critical neural substrates for correcting unexpected trajectory errors and learning from them. *Brain*, *134*(12), 3647–3661.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113.

Parsons, L. M. (2001). Exploring the functional neuroanatomy of music performance, perception, and comprehension. *Annals of the New York Academy of Sciences*, *930*(1), 211–231.

Patston, L. L. M., Hogg, S. L., & Tippett, L. J. (2007). Attention in musicians is more bilateral than in non-musicians. *Laterality*, *12*(3), 262–272.

Perreault, E. J., Kirsch, R. F., & Crago, P. E. (2002). Voluntary Control of Static Endpoint Stiffness During Force Regulation Tasks. *Journal of Neurophysiology*, *87*(6).

Przybyla, A., Good, D. C., & Sainburg, R. L. (2012). Dynamic dominance varies with handedness: reduced interlimb asymmetries in left-handers. *Experimental Brain Research*, *216*(3), 419–31.

Przybyla, A., Haaland, K. Y., Bagesteiro, L. B., & Sainburg, R. L. (2011). Motor asymmetry reduction in older adults. *Neuroscience Letters*, *489*(2), 99–104.

Rogers, M. A., Bradshaw, J. L., Cunnington, R. C., & Phillips, J. G. (1998). Inter-limb coupling in coordinated bimanual movement: Attention and asymmetries. *Laterality: Asymmetries of Body, Brain and Cognition*, *3*(1), 53–76.

Sainburg, R. L. (2005). Handedness: differential specializations for control of trajectory and position. *Exercise and Sport Sciences Reviews*, *33*(4), 206–13.

Sainburg, R. L. (2014). Convergent models of handedness and brain lateralization. *Frontiers in Psychology*, *5*, 1092.

Sainburg, R. L., & Duff, S. V. (2006). Does motor lateralization have implications for stroke rehabilitation? *Journal of Rehabilitation Research and Development*, *43*(3), 311.

Sainburg, R. L., Good, D. C., & Przybyla, A. (2013). Bilateral Synergy: A Framework for Post-Stroke Rehabilitation. *Journal of Neurology & Translational Neuroscience*, *1*(3).

Sainburg, R. L., & Kalakanis, D. (2000). Differences in Control of Limb Dynamics During Dominant and Nondominant Arm Reaching. *J Neurophysiol*, *83*(5), 2661–2675.

Sainburg, R. L., Schaefer, S. Y., & Yadav, V. (2016). Lateralized motor control processes determine asymmetry of interlimb transfer. *Neuroscience*, *334*, 26–38.

Schabowsky, C. N., Hidler, J. M., & Lum, P. S. (2007). Greater reliance on impedance control in the nondominant arm compared with the dominant arm when adapting to a novel dynamic environment. *Experimental Brain Research*, *182*(4), 567–577.

Schaefer, S. Y., Haaland, K. Y., & Sainburg, R. L. (2007). Ipsilesional motor deficits following stroke reflect hemispheric specializations for movement control. *Brain*, *130*(8), 2146–2158.

Schaefer, S. Y., Haaland, K. Y., & Sainburg, R. L. (2009). Hemispheric specialization and functional impact of ipsilesional deficits in movement coordination and accuracy. *Neuropsychologia*, *47*(13), 2953–2966.

Schaefer, S. Y., Mutha, P. K., Haaland, K. Y., & Sainburg, R. L. (2012). Hemispheric specialization for movement control produces dissociable differences in online corrections after stroke. *Cerebral Cortex*, *22*(6), 1407–1419.

Schaffer, J. E., & Sainburg, R. L. (2017). Bimanual reflexes during shared bimanual tasks are asymmetric. In *Society for Neuroscience Annual Meeting*. Washington, DC.

Semjen, A., Summers, J. J., & Cattaert, D. (1995). Hand coordination in bimanual circle drawing. *Journal of Experimental Psychology-Human Perception and Performance*, *21*(5), 1139–1157.

Serrien, D. J., Cassidy, M. J., & Brown, P. (2003). The importance of the dominant hemisphere in the organization of bimanual movements. *Human Brain Mapping*, *18*(4), 296–305.

Sherwood, D. E. (1994). Hand preference, practice order, and spatial assimilations in rapid bimanual movement. *Journal of Motor Behavior*, *26*(2), 123–134.

Sperry, R. W. (1966). Brain research: some head-splitting implications. *The Voice*, *15*, 11–16.

Spijkers, W., & Heuer, H. (1995). Structural constraints on the performance of symmetrical bimanual movements with different amplitudes. *The Quarterly Journal of Experimental Psychology*, *48*(3), 716–740.

Stucchi, N., & Viviani, P. (1993). Cerebral dominance and asynchrony between bimanual two-dimensional movements. *Journal of Experimental Psychology: Human Perception and Performance*, *19*(6), 1200.

Swinnen, S. P., Debaere, F., Puttemans, V., Vangheluwe, S., & Kiekens, C. (2002). Coordination deficits on the ipsilesional side after unilateral stroke: the effect of practice on nonisodirectional ipsilateral coordination. *Acta Psychologica*, *110*(2), 305–320.

Taylor, H. G., & Heilman, K. M. (1980). Left-hemisphere motor dominance in righthanders. *Cortex*, *16*(4), 587–603.

Todorov, E. (2004). Optimality principles in sensorimotor control. *Nature Neuroscience*, *7*(9), 907.

Treffner, P. J., & Turvey, M. T. (1995). Handedness and the asymmetric dynamics of bimanual rhythmic coordination. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(2), 318.

Treffner, P. J., & Turvey, M. T. (1996). Symmetry, broken symmetry, and handedness in bimanual coordination dynamics. *Experimental Brain Research*, *107*(3), 463–478.

Viviani, P., Perani, D., Grassi, F., Bettinardi, V., & Fazio, F. (1998). Hemispheric asymmetries and bimanual asynchrony in left-and right-handers. *Experimental Brain Research*, *120*(4), 531–536.

Volkmann, J., Schnitzler, A., Witte, O. W., & Freund, H.-J. (1998). Handedness and asymmetry of hand representation in human motor cortex. *Journal of Neurophysiology*, *79*(4), 2149–2154.

Waldron, E. M., & Anton, B. S. (1995). Effects of exercise on dexterity. *Perceptual and Motor Skills*, *80*(3), 883–889.

Walter, C. B., & Swinnen, S. P. (1990a). Asymmetric interlimb interference during the performance of a dynamic bimanual task. *Brain and Cognition*, *14*(2), 185–200.

Walter, C. B., & Swinnen, S. P. (1990b). Kinetic attraction during bimanual coordination. *Journal of Motor Behavior*, *22*(4), 451–473.

Wang, J., & Sainburg, R. L. (2007). The dominant and nondominant arms are specialized for stabilizing different features of task performance. *Experimental Brain Research*, *178*(4), 565–70.

Wetter, S., Poole, J. L., & Haaland, K. Y. (2005). Functional implications of ipsilesional motor deficits after unilateral stroke. *Archives of Physical Medicine and Rehabilitation*, *86*(4), 776–781.

Winstein, C. J., & Pohl, P. S. (1995). Effects of unilateral brain damage on the control of goal-directed hand movements. *Experimental Brain Research*.

Winter, D. A. (1990). Biomechanics and motor control of human motion. New York: Wiley-Interscience.

Woodworth, R. S. (1899). Accuracy of voluntary movement. *Psychological Review*, *3*, 1–114.

Woytowicz, E., Whitall, J., & Westlake, K. P. (2016). Age-related Changes in Bilateral Upper Extremity Coordination. *Current Geriatrics Reports*, *5*(3).

Wyke, M. (1967). Effect of brain lesions on the rapidity of arm movement. *Neurology*, *17*(11), 1113.

Yadav, V., & Sainburg, R. L. (2011). Motor lateralization is characterized by a serial hybrid control scheme. *Neuroscience*, *196*, 153–67.

Yadav, V., & Sainburg, R. L. (2014). Limb dominance results from asymmetries in predictive and impedance control mechanisms. *PloS One*, *9*(4), e93892.

Yarosh, C. A., Hoffman, D. S., & Strick, P. L. (2004). Deficits in movements of the wrist ipsilateral to a stroke in hemiparetic subjects. *Journal of Neurophysiology*, *92*(6), 3276–3285.

Yokoi, A., Hirashima, M., & Nozaki, D. (2014). Lateralized sensitivity of motor memories to the kinematics of the opposite arm reveals functional specialization during bimanual actions. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *34*(27), 9141–51.

York Haaland, K., & Delaney, H. D. (1981). Motor deficits after left or right hemisphere damage due to stroke or tumor. *Neuropsychologia*, *19*(1), 17–27.

Ziemann, U., & Hallett, M. (2001). Hemispheric asymmetry of ipsilateral motor cortex activation during unimanual motor tasks: further evidence for motor dominance. *Clinical Neurophysiology*, *112*(1), 107–113.

**Figures and Captions:**

****

**Figure 1.** Experimental Task Setup. *A:* Target display seen on the screen. *B:* Example of task condition 1. *C:* Task condition 1 hand location and target clusters. *D:* Task condition 2 hand location and target clusters.

****

**Figure 2.** Inverse Dynamics of Joint Torques. *A:* Hands connected by a spring. *B:* Spring between hands replaced by effective force of spring. *C:* Final model of arm.



**Figure 3.** Steady State Performance. (Mean ± SE) Coefficient of variation (CV) of end error for bot left (dotted line) and right (solid line) reaching arms. Each data point shows the average (±SE) of every 7 trials, or one block, across the group. Initial large difference in CV between the arms [hand by block interaction: (F(9,162) = 2.12, p = 0.0310]. Blocks 1-2 (shaded) were removed and blocks 3–10 reflect the steady-state of performance [no significant effect of block: F(7,126) = 0.37, p = 0.9179; arm: F(1,18) = 0.48, p = 0.4972; block x arm: F(7,126) = 1.18, p = 0.3209].

****

**Figure 4.** Example Kinematics and Dynamics. Representative arm movements for both task conditions, for both reaching and stabilizing arms. *Left column:* left arm reached to target, right arm stabilized. *Right column:* right arm reached and left arm stabilized. *A:* Shoulder, elbow, wrist and finger path is shown, with stick figures representing the upper arm, forearm, and hand, drawn every 2 points (~16 milliseconds). The orientation and length of the spring is shown at the start (dashed) and end (solid) of each movement. *B:* Stabilizing hand displacement, magnified in scale compared to 4A. *C & D:* Joint torque components at the elbow and shoulder, respectively, in the stabilizing arm. Spring torque = thick gray line; muscle torque = thick black line; net torque = thin black line.

****

**Figure 5.** Reaching: Kinematic Interlimb Differences. (Mean ± SE) deviation from linearity and final position error for both arms, across the 3 target clusters. *Left column:* greater deviation from linearity for the left hand-paths [F(1,19) = 32.66, p < 0.0001]. *Right column:* final position error greater for the left hand [F(1,19) = 19.42, p = 0.0003].

****

**Figure 6.** Stabilizing: Kinematic Interlimb Differences. (Mean ± SE) hand displacement and maximum spring force for the stabilizing arm across all 3 target clusters. *Left column:* right arm moved more than the left arm when stabilizing against the spring force [F(1,19) = 6.05, p = 0.0237] and both arms moved more when the reaching target was located more medially [F(2,38) = 63.96, p < 0.0001]. *Right column:* no difference in maximum spring forces between hands. [F(1,19) = 1.21, p = 0.2846], indicating that both arms experienced similar spring forces.

****

**Figure 7.** Stabilizing Arm Compliance. *A:* Endpoint compliance was greater for the right arm [F(1,19) = 6.61, p = 0.0187]. *B:* Elbow compliance of right elbow was greater than the left elbow [F(1,19) = 8.58, p = 0.0086]. *C:* Shoulder compliance was not significantly different between the arms [F(1,19) = 0.00, p = 0.9500]. Each data point represents the mean ± SE for each target cluster.