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Dynamic dominance varies with handedness: reduced interlimb asymmetries in left-handers

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Abstract

Our previous studies of interlimb asymmetries during reaching movements have given rise to the dynamic-dominance hypothesis of motor lateralization. This hypothesis proposes that dominant arm control has become optimized for efficient intersegmental coordination, which is often associated with straight and smooth hand-paths, while non-dominant arm control has become optimized for controlling steady-state posture, which has been associated with greater final position accuracy when movements are mechanically perturbed, and often during movements made in the absence of visual feedback. The basis for this model of motor lateralization was derived from studies conducted in right-handed subjects. We now ask whether left-handers show similar proficiencies in coordinating reaching movements. We recruited right- and left-handers (20 per group) to perform reaching movements to three targets, in which intersegmental coordination requirements varied systematically. Our results showed that the dominant arm of both left- and right-handers were well coordinated, as reflected by fairly straight hand-paths and low errors in initial direction. Consistent with our previous studies, the non-dominant arm of right-handers showed substantially greater curvature and large errors in initial direction, most notably to targets that elicited higher intersegmental interactions. While the right, non-dominant, hand-paths of left-handers were slightly more curved than those of the dominant arm, they were also substantially more accurate and better coordinated than the non-dominant arm of right-handers. Our results indicate a similar pattern, but reduced lateralization for intersegmental coordination in left-handers. These findings suggest that left-handers develop more coordinated control of their non-dominant arms than right-handers, possibly due to environmental pressure for right-handed manipulations.

Keywords

Left-handers; Lateralization; Coordination; Movement; Arm; Handedness

Introduction

We previously detailed interlimb asymmetries in inter-segmental coordination patterns during reaching movements in right-handers (Sainburg and Kalakanis 2000; Bagesteiro and Sainburg 2002). These findings provided the foundation for the dynamic-dominance hypothesis of motor lateralization (Sainburg 2002, 2005). In right-handers, the dominant right arm coordinates intersegmental dynamics more effectively than the non-dominant arm, as evidenced by more efficient torque strategies, smoother velocities, and straighter hand-paths. As a result, dominant arm trajectories in right-handers tend to be straight with minimal errors in initial direction, regardless of target direction (Sainburg and Kalakanis 2000; Bagesteiro and Sainburg 2002). In contrast, the non-dominant arm often shows equal or greater final position accuracy, regardless of large errors in initial direction and substantial hand-path curvatures. Previous studies suggest that the non-dominant arm appears to be more proficient in responses to inertial perturbations (Bagesteiro and Sainburg 2003) and that adaptation to novel force environments is achieved through impedance modulation, rather than through specific predictions of the applied forces (Duff and Sainburg 2007; Schabowsky et al. 2007). Taken together, these findings support the idea that the non-dominant controller is specialized for impedance control. These particular interlimb differences in sensorimotor performance were also evident in studies on interlimb transfer of visuomotor rotations, in which non-dominant arm training only improved the initial movement direction of the dominant arm and dominant arm training only improved the final position accuracy of non-dominant arm (Sainburg and Wang 2002).

The idea that interlimb differences in motor performance might reflect hemispheric specializations was tested by studies in stroke patients with unilateral hemisphere damage. We reasoned that if each hemisphere provides specialized control to each limb, then damage to either hemisphere should produce predictable deficits in the ipsilesional arm. Ipsilesional deficits in some motor functions were reported previously in both humans and animals (see Sainburg and Duff 2006 for review). Remarkably, our model was able to predict ipsilesional motor deficits in unilateral hemiparetic stroke patients, which were double dissociated by the hemisphere that was damaged (Schaefer et al. 2007, 2009a). Thus, right hemisphere damage produced deficits in final position accuracy, but not in inter-joint coordination, whereas left hemisphere damage produced deficits in coordination, but not final position accuracy. However, one major limitation of this line of research, to date, is that most of our studies were conducted in people who were right-handed.

Left-handers account for approximately 10% of total population, regardless of culture or historical time (Coren and Porac 1977; Gilbert and Wysocki 1992; McManus et al. 2010). While genetic models have suggested explanations for the skewed distribution of handedness (Annett 1972; Levy and Nagylaki 1972; McManus 1985; Klar 1996), the causes of handedness remain ambiguous (Schaafsma et al. 2009). Overall, the literature on sensorimotor performance in left-handers is limited. According to handedness inventories, left-handers as a group are more heterogonous than right-handers, with left-handers using their non-dominant arm in common daily activities more frequently than right-handers (Oldfield 1971; Bryden 1977; Borod et al. 1984). However, studies that have compared inventory results with behavioral measures suggest that inventories alone might not be sufficiently reliable tool to determine one's degree of handedness (Koch 1933; Raczkowski et al. 1974), particularly in left-handers (Benton et al. 1962; Satz et al. 1967). Thus, it appears that left-handers may not simply reflect the same patterns of hand use as that of right-handers, and it remains unclear whether patterns of motor performance asymmetries are similar to that of right-handers.

A number of previous motor performance studies in right- and left-handers have reported temporal measures, such as reaction time, and latencies of online movement corrections in both arms. In right-handers, interlimb asymmetries in reaction time are prominent, such that the left non-dominant arm shows a distinct advantage (Carson et al. 1995; Velay and Benoit-Dubrocard 1999; Boulinguez et al. 2001a; Mieschke et al. 2001). However, observations in left-handers are not as consistent. Whereas Velay and Benoit-Dubrocard (1999) showed no differences in reaction time between the limbs in left-handers, Boulinguez et al. (2001b) showed a left arm advantage, which was independent of arm dominance. These apparently contradictory results brought the measure of reaction time in studies on interlimb asymmetries into question (Goble 2007), while a recent study suggested measuring reaction time more precisely by using electromyography (Ballanger and Boulinguez 2009). Boulinguez et al. (2001a, b) provided evidence that some temporal aspects of performance, such as latencies to visual perturbations, might result from hemispheric lateralization. However, other studies have reported that the latencies of online movement corrections to visual perturbations are not asymmetric, even in right-handers (Carson et al. 1993; Shabbott and Sainburg 2009). Such findings suggest that the timing of movement initiations and corrections may not depend on handedness. Contrary to these findings, studies examining movement accuracy and adaptation have indicated that lefties show similar patterns of interlimb asymmetries to that of right-handers. A number of studies have reported advantages of the non-dominant arm in reproducing a given movement distance (Yamauchi et al. 2004) or position accuracy (Lenhard and Hoffmann 2007; Goble et al. 2009) across both right- and left-handers. This is consistent with our previous reports of final position accuracy advantages for the non-dominant arm of young healthy right-handers (Bagesteiro and Sainburg 2002; Sainburg 2002) and with final position deficits in the ipsilesional arm of right hemisphere damage stroke patients (Schaefer et al. 2007, 2009a). Our single study on left-handers to date (Wang and Sainburg 2006) showed the same patterns of interlimb transfer of visuomotor rotations to those shown in right-handers (Sainburg and Wang 2002): Opposite arm adaptation improved the spatial accuracy of only non-dominant arm movements and the initial directions of only dominant arm movements. Thus, there is substantial evidence that right- and left-handers show similar patterns of performance asymmetries between the dominant and non-dominant arms. However, because left-handers may use their non-dominant arm more for activities of daily living, it is plausible that performance asymmetries may be less pronounced in left-handers, as reflected by group handedness survey scores (Oldfield 1971; Bryden 1977; Borod et al. 1984).

In fact, brain imaging studies suggest that neural activation asymmetries may be reduced during unilateral arm use in left-handers, as compared with right-handers. Whereas high levels of neural activity in sensorimotor areas of contralateral hemisphere is always present during manual tasks across both hands and handedness groups, the level of neural activations in the ipsilateral hemisphere might be different for these two handedness groups. Some studies showed similar hemispheric asymmetry in neural activity when comparing right- to left-handers with minimal activations in ipsilateral sensorimotor cortices for dominant arm, wrist, and finger movements, but a clear tendency to increase ipsilateral activations during non-dominant arm movements (Colebatch et al. 1991; Kim et al. 1993). In agreement with these observations, Kawashima et al. (1996) reported greater ipsilateral activations during non-dominant as opposed to dominant arm movements, but only in left-handers. However, Li et al. (1996) showed that this pattern of larger ipsilateral activations during non-dominant arm movements was only significant in right-handers. Dassonville et al. (1997) quantified this asymmetry pattern as a hemispheric lateralization index, which was positively correlated with scores on the *Edinburgh Inventory* (Oldfield 1971). Thus, left-handers appear to recruit ipsilateral cortex during non-dominant arm movements more than right-handers, and left-handers tend to use their non-dominant arms for more unilateral tasks than right-handers. It is plausible that both these findings can be explained by the

right-handed bias of our cultural environment, including tools and building construction (i.e., door handles). If both groups have similar neural asymmetries, then effective manipulations with the non-dominant arm would require recruitment of ipsilateral circuitry. Integrating these results with our dynamic-dominance model, we now predict that the non-dominant arms of left-handers should show greater proficiency in coordinating intersegmental dynamics for trajectory control than that of right-handers. We now directly test this hypothesis by comparing the trajectories for reaching movements, made in directions that elicit progressively larger amplitude of interaction torques, between both handedness groups.

Materials and methods

Participants

Twenty left- (LH) and twenty right-handed (RH) volunteers, aged between 18–33 years old, were selected to this study based on self-reported handedness. Each group consisted of eight men and twelve women. All subjects were healthy and had no previous history of any musculoskeletal or neural illness that could affect arm movements. This study was conducted in accordance with the 1964 Declaration of Helsinki, and each individual signed the consent form approved by the Institutional Review Board of the Pennsylvania State University. Volunteers were financially rewarded at the minimum wage level for their participation.

Handedness questionnaire

Each participant filled out a Handedness Questionnaire adapted from Hull (1936) that included 35 questions about hand usage for manual activities such as throwing, writing, jar opening, etc. Each question requires one answer out of three (right, left, or either) choices for each listed task, indicating the preferred hand for that task: right (score: 1), left (score: -1), or either (score: 0). Scores from all 35 questions were summed, and handedness, in terms of hand preference for a given task, was calculated as a percentage response, where 100 represents an absolute right-hander and -100 an absolute left-hander. In essence, this inventory by Hull (1936) reflects an extended set of tasks, similar to those listed in the Edinburgh inventory (Oldfield 1971). Our rationale for using the Hull inventory is that we believe that the extended number of tasks might allow more gradations in our measure of handedness.

Experimental setup

The experimental setup is shown in Fig. 1. We provided veridical feedback of cursors (small circle with a cross hairline, $d = 0.016$ m) that represented the tip of index finger of each arm. These cursors were projected from commercially available 52" HDTV onto a mirror, which covered the subjects' arms. All joints, in both arms, distal to the elbow, were splinted to restrict subjects' motions to two segments: upper arm and forearm. The upper arms were free to move with scapular and trunk motion, which was only restricted by the table position relative to the subject. Subjects' forearms were supported on air sleds that minimized the effects of gravity and friction on segment motion. The air sled support system also minimizes physical fatigue. Four (2 per arm) six-degree-of-freedom electromagnetic sensors (Ascension Technology, USA) provided displacements of both upper arm and forearm in both right and left arms. For this purpose, we digitized the following anatomical landmarks in each arm: proximal interphalangeal joint, lateral epicondyle of the humerus, and acromion, directly posterior to the acromioclavicular joint. Data were recorded at the sampling frequency of 130 Hz using our software developed in REALbasic 2008 (REAL Software, Inc., USA).

Experimental design

Targets—We designed three targets in order to systematically vary the intersegmental joint coordination requirements. For each arm, the starting circle ($d = 0.020$ m) location was determined based on joint configurations of 90° and 20° for the elbow and shoulder, respectively. The elbow angle was defined as the angle between upper arm and forearm, and the shoulder angle as the angle between the coronal plane and upper arm. While all targets required 20° of elbow extension, each of three targets required different amounts of shoulder excursion: 0° , 10° , and 20° , respectively. Thus, the first target (0) required only elbow motion, while the last (20) required equal joint excursions at the shoulder and elbow. We previously showed that interaction torques that arise between the segments of the moving limb are largest for the 20 target, and least for the 0 target (Sainburg and Kalakanis 2000). It should also be stressed that because the proximal end of the upper arm was free to translate in space with scapular and trunk motion, and it was possible to achieve task accuracy without perfectly performing the designed joint excursions. We allowed this freedom because restricting shoulder motion is uncomfortable for subjects and may substantially alter the kinematic profiles of the segments. All targets were presented as bull-eye type (Fig. 1, top view) circle ($d = 0.028$ m).

Task—Each individual performed 180 rapid unimanual reaching movements, switching arms after every 18 trials. Every block of 18 trials consisted of 6 movements to each one of three targets presented in pseudo-random order with no two consecutive trials to the same target. Note that the first block of trials for each arm was treated as task-familiarization routine, and thus was not included in data analysis. Subjects moved on the audio single tone “go” signal, which occurred when the cursor was positioned and remained within the start circle for 0.3 s. Visual feedback of the cursor was removed when it breached the start circle. The rationale for removing visual feedback was that interlimb differences in coordination have been shown to be greatest under no visual feedback conditions (Sainburg 2002). We set the trial duration to 1 s, and all these rapid movements were completed well within that time. After each trial, final position of cursor was displayed for 1 s to provide feedback about accuracy. This position was determined as the first point in which the hand tangential velocity slowed down below 0.02 m/s (near zero). In order to encourage focused attention to the task throughout the session, points for accuracy were awarded after each trial, and a cumulative score was updated on the top of the screen. In order to assure rapid and consistent speed of movements, velocity feedback was provided with a thermometer style display. When movements were within the velocity boundaries of 0.7–1.2 m/s, subjects were awarded points that depended on the distance of the final position from the center of the target.

Data analysis

Data processing—Data were processed and analyzed using IgorPro 6.0 (WaveMetrics, Inc., USA) software. Time series were low-pass filtered at 8 Hz using a zero phase 6th order Butterworth filter. For analysis, movement initiation and completion were identified as the first local minima on the velocity profile below the threshold of 8% of the peak tangential velocity. While this algorithm was found to work well for majority of trials ($>90\%$), a manual correction based on the visual inspection of the tangential velocity profiles was necessary in some cases.

Movement kinematics—The following kinematic- and temporal-dependent measures were quantified for each movement: shoulder and elbow joint excursion at movement end, peak tangential velocity, hand-path linearity, initial direction error, accuracy, and precision measures in two-dimensional space. Shoulder and elbow joint excursions were defined as the difference in joint angles between movement initiation and completion. Hand-

path linearity was defined as the ratio between the minor and the major axis. The major axis was defined as the longest distance between any two points on the hand-path, and the minor axis was defined as the longest distance from any given point on the hand-path perpendicular to major axis. This measure of linearity would yield 0.5 for a semicircle path and zero for a straight-line path. Initial direction error was defined as the angular difference between target direction and movement direction at the time of peak tangential velocity. Absolute error in two-dimensional space, a measure of accuracy, was calculated as the *Euclidean* distance from position of the index fingertip at movement completion (x_f, y_f) to the center of the target (x_t, y_t):

$$d = \sqrt{(x_t - x_f)^2 + (y_t - y_f)^2}.$$

Two-dimensional precision error (2DPE), a measure of precision, was calculated for a given trial as the *Euclidean* distance from the position of the index fingertip at movement completion of that trial (x_f, y_f) to the mean position of the index fingertip at movement completion (x_m, y_m):

$$d = \sqrt{(x_m - x_f)^2 + (y_m - y_f)^2}.$$

This mean position of the index fingertip at movement completion (x_m, y_m) was calculated by averaging the x and y coordinates of the index fingertip at movement completion across all trials within each target for each subject.

Inverse dynamics analysis—Joint torques were quantified using the method described by Schneider and Zernicke (1990). Kinematic recordings were made in three dimensions, and each limb was modeled as a set of 2 interconnected, planar rigid links with frictionless joints (shoulder and elbow). In order to simplify the kinetic analyses and maintain the accuracy of the data, a planar model of limb intersegmental dynamics was employed, where the analysis was restricted to the moving-local plane containing the limb segments. The terms in the equations of motion were partitioned into three main components: net torque, muscle torque, and interaction torque (Bagesteiro and Sainburg 2002). The net torque is directly proportional to joint acceleration and equal to the sum of the muscle and interaction torques. Interaction torque at a joint represents the rotational effects of forces due to the motion of other body segments, while muscle torque primarily represents the rotational effects of muscle forces. It should be realized that in the case of this study, interaction torque generated at the elbow was primarily related to shoulder rotational accelerations and velocities, as motions of body segments proximal to the shoulder were constrained by a trunk belt. However, any motion of the body was reflected by our measure of shoulder point acceleration, and thus is included in our interaction torque. Limb segment inertia, center of mass location, and mass were computed using subjects body weight and limb segment lengths (Winter 1990). In order to examine variation of intersegmental coordination requirements across our targets, we summed peak interaction torques that occurred at elbow and shoulder joint during the initial phase of movement (up to peak tangential acceleration).

Statistics—The means of individual dependent measures were subjected to 3-way repeated measures mixed-factor analysis of variance (ANOVA) with handedness group (right-handers = RH and left-handers = LH) as a between-subject factor, and arm (dominant = D and non-dominant = ND) and target (0°, 10° and 20° of shoulder flexion) as the within-subject factors. Significant interactions and main effects were subjected to post-hoc analysis

using the Student's *t* test. 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 $\pm$ standard error. A linear regression was used to test correlations between either the mean individual interlimb differences (ID = right – left) or laterality index (LI = (right – left)/(right + left)) in hand-path curvature (a proxy for intersegmental coordination) and degree of handedness. Statistical analysis was performed using the JMP statistical package (JMP 8.0, SAS Institute Inc., Cary, NC, 1989–2011).

Results

Handedness

Prior to statistical analysis, we flipped the sign in our LH group's handedness scores to compare the strength of dominant hand preference between the RH and LH groups. In order to apply appropriate statistics to our RH vs. LH group comparison, we first found that according to the Goodness-of-Fit Test, both data sets (RH: $P < 0.0189$ and LH: $P < 0.0186$, Shapiro–Wilk *W* Test) did not reflect a normal distribution. We also found that the variances of both RH and LH group data sets were not equal ($F_{(1,19)} = 13.05$, $P = 0.0009$, Levene Test) with the standard deviation significantly higher in the LH group (41.7 vs. 15.9). We, therefore, used a non-parametric analysis for comparison. Overall, our LH subjects showed significantly lower dominant hand preference scores than did our RH group (46 ± 9 vs. $83 \pm 4\%$; $P = 0.0011$, Wilcoxon Test). The range of hand preference scores was higher in our LH group (+29 to –94%) than in our RH group (+49 to +100%). While four out of twenty left-handers showed slightly higher preference for the right non-dominant arm, these scores (< 30) were well below the minimum found in RH group (min = 49%). Overall, these results indicate that our LH group had substantially lower preference for dominant arm use than did our RH group. This is consistent with previous reports of left-handed populations (Oldfield 1971).

Validity of task design

We designed this task in order to systematically vary the intersegmental dynamic requirements of the task between the three targets, by requiring the same amount of elbow excursion (20°), but varying the required shoulder excursion between targets. Our targets are named according to the shoulder excursion required: Target 0 required no shoulder excursion, while target 20 required 20° of shoulder excursion. We expected this design to elicit substantially larger interaction torques, across the joints, at the 20° target than at the 0° target. Figure 2 shows the mean magnitude of peak interaction torque (PIT) summed across the joints (see “Methods”) for each arm and each target in both handedness groups. As shown in Fig. 2, PIT increased by nearly 300% across targets, from approximately 2 Nm at target 0 to approximately 6 Nm at target 20. In addition, PIT was well matched across arms and handedness groups (see Fig. 2). According to our 3-way mixed factor ANOVA, there was no significant 3-way interaction ($F_{(2,190)} = 0.28$, $P = 0.75$) and no effect of arm ($F_{(1,190)} = 0.61$, $P = 0.44$) nor handedness group ($F_{(1,190)} = 0.28$, $P = 0.60$). As described above, we found a main effect of target ($F_{(2,190)} = 213.48$, $P < 0.0001$) on PIT. Note that PIT was summed across elbow and shoulder joints (see “Methods”), and the effects of motion of the more proximal body segments were reflected by the contributions to shoulder linear accelerations. In addition, contributions from wrist and finger motion were eliminated by rigidly splinting the wrist and hand. Movement of the trunk was minimized or eliminated by restraining subjects' torso with straps. Our inverse dynamics analysis took account of both trunk and wrist motions that might have occurred, despite our restraints. Thus, both shoulder linear accelerations and wrist rotations were quantified and included in our equations of motion.

We were also successful at insuring that movement speed did not change significantly across hand or handedness group. However, speed varied systematically with movement direction, as reported in previous literature (Gordon et al. 1994; Sainburg and Kalakanis 2000; Bagesteiro and Sainburg 2002). This dependence is related to configuration-dependent variations in limb inertia that occur across movement directions. As expected by our design, speed decreased for movement directions that required greater shoulder excursions, which have greater inertial resistance (target 0: 0.91 ± 0.01 > target 10: 0.75 ± 0.02 > target 20: 0.69 ± 0.01). While our 3-way ANOVA confirmed this effect of target on movement speed ($F_{(2,95)} = 210.34$, $P < 0.0001$), there were no significant 3-way interactions ($F_{(2,190)} = 1.26$, $P = 0.29$), and there was no effect of arm ($F_{(1,190)} = 0.04$, $P = 0.84$) nor handedness group ($F_{(1,190)} = 0.11$, $P = 0.74$) on movement speed.

These findings confirmed that our experimental design systematically changed intersegmental coordination requirements of the task across targets. Both speed and intersegmental requirements, measured as interaction torque magnitude, varied systematically across targets, but were matched across arms and handedness groups.

Interlimb differences in movement coordination

We quantified hand-path curvature and initial direction errors as proxies for movement coordination. Figure 3 shows examples of hand-paths for movements performed to each target by a RH and a LH subject, using both the dominant (D) and the non-dominant (ND) arm. For both subjects, the movement to targets 0 and 10, with lower interjoint coordination requirements, were fairly straight regardless of hand. However, the hand-paths from movements to target 20, which elicited the largest interaction torques, varied depending on hand. The dominant hand-path is fairly straight, whereas the non-dominant hand-path is initially directed laterally, before curving back toward the target. We previously detailed how this type of hand-path profile is related to a failure to efficiently coordinate muscle actions with interaction torques (Sainburg and Kalakanis 2000; Bagesteiro and Sainburg 2002) and is characteristic of non-dominant coordination in right-handers. It should be noted, however, that the non-dominant arm of the left-hander is slightly less curved than that of the right-hander.

The consistency of these findings across subjects is demonstrated by the graphs of mean ($\pm$ SE) in Fig. 4. This figure shows measures of hand-path curvature for each target and arm across subjects in RH and LH group. Our 3-way mixed model ANOVA revealed a significant 3-way interaction ($F_{(2,190)} = 3.63$, $P = 0.03$). While there was a significant effect of target ($F_{(2,190)} = 3.83$, $P = 0.02$) and a significant interaction between target and hand ($F_{(2,190)} = 11.14$, $P < 0.0001$), the interaction between handedness group and hand was not significant ($F_{(2,190)} = 0.92$, $P = 0.34$). Post-hoc analysis revealed that within each handedness group, interlimb differences in hand-path curvature to targets 0 and 10 were insignificant, while those to target 20 were significantly different for both groups. It should be stressed that the amplitude of these differences for left-handers was somewhat smaller than for right-handers (see Fig. 4). In fact, for right-handers, the hand-path curvature for non-dominant arm movements to target 20 was 72% larger than that of the dominant arm (0.110 ± 0.009 vs. 0.064 ± 0.005 , $T_{(190)} = 6.16$, $P < 0.0001$, Student's *t* test). In left-handers, the mean difference between dominant and non-dominant arms was on average only 32% (0.079 ± 0.010 vs. 0.060 ± 0.004 , $T_{(190)} = 2.58$, $P = 0.01$, Student's *t* test).

Thus, both left- and right-handers showed a significant difference between dominant and non-dominant arm coordination that depended on target, such that movements that elicited larger interaction torques showed substantial interlimb differences in coordination. In addition, the mean amplitude of these differences was larger for right- rather than left-handers. The reduced interlimb difference in hand-path curvature in left-handers was due to

straighter movements of the non-dominant arm, as compared to right-handers. In fact, dominant hand-paths were not different between groups (0.060 ± 0.004 vs. 0.064 ± 0.005 , $T_{(190)} = 0.65$, $P = 0.52$, Student's t test), while non-dominant hand-paths were significantly different between left- and right-handers.

As expected, we found a similar pattern for our measure of initial direction error. Figure 5 shows initial direction errors averaged for each target and arm across subjects in both RH and LH groups. Regardless of target direction, the differences in initial directional accuracy between the dominant arms of RH and LH group were not significant (target 0: -7.6 ± 0.9 vs. -7.1 ± 1.0 , $T_{(190)} = 0.32$, $P = 0.75$; target 10: -3.9 ± 1.3 vs. -2.8 ± 1.1 , $T_{(190)} = 0.61$, $P = 0.54$; target 20: -0.3 ± 1.4 vs. 1.3 ± 1.1 , $T_{(190)} = 0.89$, $P = 0.37$, Student's t test). In contrast, non-dominant arm performance in right-handers showed higher errors in the directions with larger intersegmental dynamics (target 10: 5.5 ± 0.9 vs. -3.9 ± 1.3 , $T_{(190)} = 5.25$, $P < 0.0001$; target 20: 5.1 ± 1.5 vs. -0.3 ± 1.4 , $T_{(190)} = 3.01$, $P < 0.003$, Student's t test). This was not the case for our LH group, in which the differences between the arms were not significant (target 10: -0.4 ± 1.6 vs. -2.8 ± 1.1 , $T_{(190)} = 1.36$, $P = 0.17$; target 20: 2.9 ± 1.9 vs. 1.3 ± 1.1 , $T_{(190)} = 0.84$, $P = 0.40$, Student's t test). For target 0, with the smallest intersegmental interactions, neither RH (-7.6 ± 0.9 vs. -5.2 ± 1.2 , $T_{(190)} = 1.35$, $P = 0.18$, Student's t test) nor LH (-7.1 ± 1.0 vs. -9.1 ± 1.2 , $T_{(190)} = 1.15$, $P = 0.25$, Student's t test) groups showed significant differences in direction errors between the arms. Taken together with our results for hand-path curvature, our findings provide convergent evidence that interlimb differences in coordination for left-handers are generally reduced, and that this increased symmetry results from apparent coordination advantages of the non-dominant arm.

Overall, these results confirm that left-handers show similar dominant arm advantages in intersegmental coordination, as compared to right-handers. Interestingly, these interlimb differences were lower in left-handers, suggesting that left-handers may be less lateralized in their motor behavior.

Relationship of hand preference to hand-path curvature

As shown above, the results of our handedness survey indicated that left-handers had lower hand-preference scores, on average, than right-handers. In fact, hand preference, as measured by the handedness inventory (Hull 1936), was 45% lower in left- than in right-handers. It is possible that this reduction in hand preference for left-handers might explain our kinematic results, which showed significantly lower interlimb differences for this group. To test this hypothesis, we regressed interlimb differences in hand-path curvature, for movements made to target 20, against each subjects' handedness survey score. However, for both groups of subjects, this regression was not significant: LH ($r^2 = 0.02$, $P = 0.51$), RH ($r^2 = 0.06$, $P = 0.15$), and nor was it significant when we pooled the data across both groups of subjects ($r^2 = 0.08$, $P = 0.07$). This latter case is shown in Fig. 6. We also computed this regression after excluding left-handers with low (or negative) scores and found that even the left-handers with the higher (>50%) hand-preference scores showed no correlation between extent of handedness and interlimb difference in movement curvature ($r^2 = 0.17$, $P = 0.12$). We also computed the correlation between handedness score and a more standard computation of laterality index for hand-path curvature (RH – LH/RH + LH). While this measure provided a normalized difference in hand-path curvature between right and left arm movements, it also did not correlate with handedness score (RH group: $r^2 = 0.03$, $P = 0.22$; LH group: $r^2 = -0.06$, $P = 0.98$; both groups: $r^2 = 0.04$, $P = 0.10$).

Task accuracy

We quantified task accuracy using absolute error and 2D precision error (2DPE) computed in two-dimensional space (see "Methods"). We did not find 3-way interactions for either

absolute error ($F_{(2,190)} = 0.12$, $P = 0.88$) nor 2D precision error ($F_{(2,190)} = 0.07$, $P = 0.93$). However, for absolute error, we found a significant 2-way interaction between handedness group and arm ($F_{(1,190)} = 5.24$, $P = 0.02$). Figure 7 shows the nature of this interaction: while the dominant arms of right-handers were not significantly different than left-handers (0.028 ± 0.002 vs. 0.027 ± 0.002 , $T_{(190)} = 0.49$, $P = 0.62$, Student's t test), the non-dominant arm of the left-handed group was significantly more accurate than that of the right-handed group (0.025 ± 0.002 vs. 0.031 ± 0.002 , $T_{(190)} = 3.73$, $P = 0.0003$, Student's t test). This finding is consistent with our findings for hand-path curvature, in which left-handers had straighter non-dominant arm movements than right-handers. In terms of 2D precision error (see Fig. 8), there was a main effect of target ($F_{(2,190)} = 5.58$, $P = 0.004$), but no interactions with handedness group ($F_{(1,190)} = 0.37$, $P = 0.69$) nor arm ($F_{(1,190)} = 0.02$, $P = 0.98$). When averaged across subjects, handedness groups and arms, targets 0 and 20 were not significantly different (0.016 ± 0.002 vs. 0.016 ± 0.002 , $T_{(190)} = 0.03$, $P = 0.97$, Student's t test), but target 10 was significantly smaller than both target 0 (0.014 ± 0.001 vs. 0.016 ± 0.002 , $T_{(190)} = 2.87$, $P = 0.005$, Student's t test) and target 20 (0.014 ± 0.001 vs. 0.016 ± 0.002 , $T_{(190)} = 2.91$, $P = 0.004$, Student's t test).

Overall, our findings indicate that both left- and right-handers show similar patterns of interlimb asymmetry in movement coordination, as reflected by hand-path curvature, as well as in movement accuracy. However, while left-handers show similar curvatures and accuracies as right-handers for their dominant arm, non-dominant arm movements of left-handers tend to be straighter and more accurate than the non-dominant arms of right-handers.

Discussion

The purpose of this study was to test hypothesis that interlimb differences in intersegmental coordination depend on handedness. We explored coordination differences in kinematics and dynamics across both dominant and non-dominant arms in both right- and left-handers who self-reported their degree of handedness using the extended 35-item version of the handedness survey adapted from Hull (1936).

Interlimb differences in coordination are similar in left- and right-handers

Our results indicate that left-handers show similar inter-limb coordination differences to that of right-handers. We have previously shown in right-handers that the right arm/ left hemisphere system is specialized for coordination of intersegmental dynamics, as reflected by trajectory curvatures that do not vary with interaction torque amplitude (Sainburg and Kalakanis 2000; Bagesteiro and Sainburg 2002; Sainburg and Wang 2002; Schaefer et al. 2007, 2009b). Our current findings extend this observation to left-handers. Our results indicate that left-handers make substantially straighter and more accurate movements with their left dominant arm than with the right non-dominant arm, and that these interlimb differences increase in movement directions that elicit progressively larger interaction torques. Furthermore, both left- and right-hand groups showed similar coordination profiles with their dominant arms. These findings not only support our dynamic-dominance hypothesis of motor lateralization (Sainburg 2002, 2005) but also indicate that this unique motor specialization is dependent on handedness. This is contrary to previous studies that explored the effects of handedness on the timing of movement initiation. Boulinguez et al. (2001b) showed a left arm advantage in the timing of movement initiation across both handedness groups, indicating that such timing may depend on a hemisphere advantage, but not on handedness per se'. Other features of performance that have been shown to vary with handedness, rather than hemisphere, include proprioceptive matching, accuracy, and interlimb transfer of visuomotor adaptation. Two previous studies have shown advantages in proprioceptive matching, a measure of sensory resolution that depend on handedness

(Yamauchi et al. 2004; Goble et al. 2009). In both cases, the non-dominant arm (left for righties and right for lefties) was consistently better than the dominant arm (right for righties and left for lefties) across both handedness groups. Furthermore, Lenhard and Hoffmann (2007) revealed a non-dominant arm advantage in spatial accuracy of reaching movements across both handedness groups. Our current findings are also consistent with our previous reports on interlimb transfer of visuomotor rotations: In both left- and right-handed groups, opposite arm training improved the initial movement direction of only the dominant arm and the spatial accuracy of only the non-dominant arm (Wang and Sainburg 2006). Overall, our current findings support and extend previous studies that have revealed aspects of motor behavior that vary with handedness. In this study, we confirm that dominant arm advantages in intersegmental coordination are robust in both left- and right-handers.

Reduced behavioral lateralization in left-handers

Our findings indicate that left-handers show reduced interlimb differences in measures of movement curvature, initial direction error, accuracy, and precision. In right-handers, we have consistently shown that interlimb differences in movement curvatures increase across directions, as the amplitude of intersegmental dynamics become larger (Sainburg and Kalakanis 2000; Bagesteiro and Sainburg 2002). In the current study, we report the same pattern of interlimb differences for left-handers. However, the amplitude of the differences between the arms is substantially smaller in left- than right-handers. This is attributable to a reduction in the amplitude of movement errors and curvature with the non-dominant arm, when compared to the right-handed group, while the dominant arm measures are similar between groups. This result is in agreement with Kilshaw and Annett (1983), who compared performance of left- and right-handers on a pegboard task. The left-handed subjects performed the task with their right non-dominant arm in significantly shorter time than right-handers with their left non-dominant arm. Such findings are consistent with the results of handedness inventories, which have also reported reduced lateralization in left-handers (Hull 1936; Oldfield 1971). Our current findings extend these previous studies by showing that this reduced lateralization in left-handers can be quantified by discrete measures associated with coordination of intersegmental dynamics. It is plausible that this reduction in lateralization of left-handers is related to environmental stresses, requiring more elaborate use of the right non-dominant arm over the course of one's life; for example, the geometrical orientation of a typical door requires right-hand manipulations, whether one is left- or right-handed. We expect that daily exposure to a world of right-handed implements might create sufficient pressure for voluntary use of the right non-dominant arm for tasks that typically are completed with the dominant arm. In fact, the results of our handedness inventory indicate that our left-handed group reported approximately 3 times higher usage of the non-dominant arm than our right-handed group, a finding consistent with previous studies (Hull 1936; Oldfield 1971). Although we did not follow up our questionnaire with further behavioral measures of hand preference (Koch 1933; Benton et al. 1962; Satz et al. 1967; Raczkowski et al. 1974), it is unlikely that this difference is due to inaccuracies in self-reported hand usage. Instead, we expect that our left-handers have both increased patterns of non-dominant arm usage, as compared to right-handers, and that this is reflected by reduced differences in coordination and accuracy, as reflected by our measures of hand-path curvature and position error.

As noted above, our findings for extent of lateralization of our right- and left-handed groups show similar patterns for the group means of our handedness inventory and the group means for our coordination index, hand-path curvature. However, the individual measures from the handedness inventory and from our coordination index were not correlated. It has been suggested that subjects' self-report on an inventory can be at odds with their performance of tasks, such as writing (Chapman and Chapman 1987) and a range of other manual tasks

(Koch 1933; Benton et al. 1962; Satz et al. 1967; Raczkowski et al. 1974; Hebbal and Mysorekar 2006). Our current data suggests that handedness inventories can be effective for group categorization of handedness, but identifying individual levels of motor lateralization may require measures of performance, rather than self-report.

Movement accuracy

Our index of coordination, movement curvature, showed similar trends for left- and right-handed groups: (1) interlimb differences in curvature increased across directions as interaction torque amplitude increased, and that (2) for the target that elicited the largest interaction torques, non-dominant arm movements were substantially more curved than dominant arm movements, and (3) these interlimb differences were largest for right-handers. However, our measure of movement accuracy and absolute final position error showed a different trend: (1) For right-handers, dominant arm movements were slightly more accurate than non-dominant arm movements. (2) For left-handers, non-dominant arm movements were slightly more accurate than dominant arm movements. (3) Dominant arm accuracy was similar across groups, while non-dominant arm accuracy was greater for the left-handers group. The strongest trend was the greater accuracy of the non-dominant arm of left-handers, as compared to that of right-handers.

It should be noted that we have previously reported advantages in movement accuracy of the non-dominant arm in right-handers for movements made without visual feedback (Sainburg and Kalakanis 2000) and most recently in paradigms with multiple targets covering a large work-space (Przybyla and Sainburg, 2010 Society for Neuroscience abstract). Similarly, Lenhard and Hoffmann (2007) showed greater accuracy in the non-dominant arms of both handedness groups for reaching movements made with higher precision requirements than the current task. The non-dominant arm of both handedness groups has also been shown to match proprioceptive targets with greater accuracy (Yamauchi et al. 2004; Goble et al. 2009). However, in the current study, such a non-dominant advantage in accuracy only occurred for the left-handers. In fact, we have previously shown that the non-dominant arm advantage for spatial accuracy becomes reduced for movements that elicit large intersegmental interaction torques (Bagesteiro and Sainburg 2002). We attributed this to the fact that non-dominant coordination fails to adequately account for interaction torques, resulting in large trajectory deviations, which ultimately degrade final position accuracy. In fact, in the current study, the greatest trajectory curvatures occurred for the non-dominant arm of right-handers, consistent with the interpretation that these larger trajectory deviations degraded right-hander's final position accuracy.

Both hemispheres are required for integrated motor control

Our model of motor lateralization proposes that each hemisphere has become specialized for different aspects of motor control. We propose that the left hemisphere in right-handers is specialized for predicting and controlling task dynamics, while the right hemisphere is specialized for control of positional impedance, as required to achieve a steady-state limb position. According to this idea, integrated control of each arm requires processes from both hemispheres. Each limb is conferred with behavioral advantages due to its greater sensorimotor connectivity with contralateral cortex. This hypothesis has been supported by studies in stroke patients that have predicted hemisphere-specific deficits in the ipsilesional arm (the arm on the same side as the brain lesion). Whereas this arm is often considered unaffected by sensorimotor stroke, because it does not exhibit paresis or spasticity, persistent deficits in accuracy and coordination have previously been documented (Winstein and Pohl 1995; Haaland et al. 2004). Furthermore, we have shown that these deficits vary with the side of damage and are predicted by our model of motor lateralization (Schaefer et al. 2007, 2009a, b; Mutha et al. 2010, 2011). Specifically, in right-handers, right hemisphere

stroke produces deficits in positional accuracy, while left hemisphere lesions produce deficits in coordination of intersegmental dynamics. Furthermore, these deficits are both persistent through time, and substantially limit patients' functional performance (Desrosiers et al. 1996; Schaefer et al. 2009b). These findings emphasize the importance of ipsilateral hemisphere in coordinating unilateral arm movements. However, such studies have not assessed formerly left-handed stroke patients, due to the difficulties in recruiting adequate numbers of such patients.

Brain imaging studies have demonstrated substantial recruitment of ipsilateral cortex during unilateral arm movements in both right- and left-handers. Furthermore, these studies have revealed that the most robust activations during arm and finger movements are seen in contralateral sensorimotor cortices, which is consistent with anatomical studies in non-human primates (for example, Brinkman and Kuypers 1972) as well as electrophysiology in humans (for example, Penfield and Boldrey 1937). However, unilateral movements also have been shown to substantially activate ipsilateral motor and premotor cortices, even when making distal finger movements, which are innervated largely through contralateral corticospinal projections (Kim et al. 1993; Li et al. 1996; Dassonville et al. 1997; Kawashima et al. 1997; Singh et al. 1998; Solodkin et al. 2001; Verstynen et al. 2005). Dassonville et al. (1997) identified a correlation between the extent of ipsilateral activation and the extent of handedness, estimated by the Edinburgh inventory (Oldfield 1971). These findings suggested that the extent of ipsilateral cortex activation is associated with reduced behavioral laterality, a result consistent with the concept of hemispheric specialization: If each hemisphere is specialized for different aspects of performance, then recruitment of both hemispheres should be associated with reduced performance asymmetries. In fact, Dassonville et al. (1997) also showed that left-handers tend to show reduced laterality, as measured by the Edinburgh inventory, and that this is associated with more symmetric hemispheric activations during finger movements. While it has been argued that the use of Handedness Inventories alone might not be adequate to assess handedness due to the differences between answering questionnaires and behavioral measures (Koch 1933; Benton et al. 1962; Satz et al. 1967; Raczkowski et al. 1974), our current findings support those of Dassonville et al. (1997) by indicating reduced lateralization in left-handers through quantifying patterns of coordination between the arms. Overall, the findings that unilateral arm and finger movements recruit bilateral sensorimotor cortex activity are consistent with the concept of neural lateralization, in which each hemisphere has become specialized for different aspects of control. This type of neural organization would necessitate that unilateral arm and hand movements should require activations from both hemispheres, in order to recruit each hemisphere's specialized control processes.

Given that both hemispheres are recruited for unilateral arm control, should the decreased behavioral lateralization of left-handers reported in this and earlier studies reflect differences in neural lateralization? We consider it most likely that left-handers have similar patterns and extents of neural lateralization as right-handers. However, different patterns of arm use may result in different recruitment profiles for left-handers, such that they recruit ipsilateral cortex more extensively during non-dominant arm use than do right-handers. In other words, each hemisphere contains specialized circuitry for control of different features of movement. Because left-handers must use the right arm more often, they become more adept at recruiting ipsilateral (right) cortex, and the right (non-dominant) arm can then coordinate intersegmental dynamics more effectively. This idea is supported by previous brain imaging studies of left- and right-handed subjects: Kawashima et al. (1997) and Solodkin et al. (2001) showed relatively higher increase in ipsilateral activity in the right, non-dominant, arm of left-handers when comparing to the left, non-dominant, arm of right-handers. We suggest that this pattern of activity is due to similar patterns of neural specialization, but accounts for the reduced behavioral lateralization observed in left-handers that is associated

with better coordination of the right non-dominant arm. We conclude that left-handers are less behaviorally lateralized due to more efficient coordination with their non-dominant arms. Based on the findings described above, we expect that this pattern of behavioral lateralization is due to greater neural recruitment of ipsilateral cortex and not due to differences in the extent of hemispheric specialization for motor control. However, more research is necessary to distinguish between these alternatives.

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Fig. 1. Experimental setup with targets labeled 0, 10, and 20 for 0°, 10°, and 20° of shoulder flexion, respectively, with constant 20° of elbow extension

Fig. 2. Mean ($\pm$ SE) magnitude of peak interaction torque summed across the joints for the dominant (D) and the non-dominant (ND) arm and for each target (0, 10, 20) in both right- (*white*) and left-handed (*black*) group

Fig. 3.

Examples of typical hand-paths for movements performed to each target (0, 10, 20) by a right- and a left-handed subject, using both the dominant and the non-dominant arm; note larger hand-path curvatures for non-dominant arms in movements to target 20 in these exemplar trials for both right-handers (0.132 vs. 0.055) and left-handers (0.085 vs. 0.061)

Fig. 4. Mean ($\pm$ SE) hand-path curvature for the dominant (D) and the non-dominant (ND) arm and for each target (0, 10, 20) in both right- (*dashed*) and left-handed (*solid*) group

Fig. 5. Mean ($\pm$ SE) initial direction errors for the dominant (D) and the non-dominant (ND) arm and for each target (0, 10, 20) in both right- (*dashed*) and left-handed (*solid*) group

Fig. 6.
Line of best fit for mean individual interlimb differences in hand-path curvature vs. hand preference

Fig. 7. Mean ($\pm$ SE) absolute error across targets for the dominant (D) and the non-dominant (ND) arm in both right- (*dashed*) and left-handed (*solid*) group

Fig. 8. Mean ($\pm$ SE) two-dimensional precision error across targets for the dominant (D) and the non-dominant (ND) arm in both right- (*dashed*) and left-handed (*solid*) group