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Lateralized Motor Control Processes Determine Asymmetry of Interlimb Transfer

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Abstract

This experiment tested the hypothesis that interlimb transfer of motor performance depends on recruitment of motor control processes that are specialized to the hemisphere contralateral to the arm that is initially trained. Right-handed participants performed a single-joint task, in which reaches were targeted to 4 different distances. While the speed and accuracy was similar for both hands, the underlying control mechanisms used to vary movement speed with distance were systematically different between the arms: The amplitude of the initial acceleration profiles scaled greater with movement speed for the right-dominant arm, while the duration of the initial acceleration profile scaled greater with movement speed for the left-non-dominant arm. These two processes were previously shown to be differentially disrupted by left and right hemisphere damage, respectively. We now hypothesize that task practice with the right arm might reinforce left-hemisphere mechanisms that vary acceleration amplitude with distance, while practice with the left arm might reinforce right-hemisphere mechanisms that vary acceleration duration with distance. We thus predict that following right arm practice, the left arm should show increased contributions of acceleration amplitude to peak velocities, and following left arm practice, the right arm should show increased contributions of acceleration duration to peak velocities. Our findings support these predictions, indicating that asymmetry in interlimb transfer of motor performance, at least in the task used here, depends on recruitment of lateralized motor control processes.

INTRODUCTION

Patterns of generalization have provided information about how motor learning might be represented in the central nervous system. Generalization of learning across the limbs has the added advantage of providing information that can be exploited in rehabilitation of

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unilateral disorders of movement, such as stroke (Dragert and Zehr, 2013, Yoo et al., 2013, Urbin et al., 2015). However, the literature on interlimb transfer of motor learning is replete with seemingly contradictory findings. A number of previous studies have reported asymmetries in interlimb transfer that depend on whether the dominant or non-dominant arm is initially trained, suggesting that hemispheric lateralization can predict the direction of interlimb transfer (Sainburg and Wang, 2002b, Criscimagna-Hemminger et al., 2003, Wang and Sainburg, 2004b, 2006b, Galea et al., 2007, Chase and Seidler, 2008, Lefumat et al., 2015). However, other studies have reported that handedness has no influence on transfer of motor practice effects across the arms (Balitsky Thompson and Henriques, 2010, Stockinger et al., 2015).

While earlier studies tended to examine transfer of tasks such as finger tapping (Laszlo et al., 1970) keyboard pressing (Taylor and Heilman, 1980), and writing (Parlow and Kinsbourne, 1989, 1990), more recent studies have focused on adaptation to environmental perturbations during reaching, a paradigm that allows for the quantification of the extent of transfer, as well as assessing the coordinate system governing transfer. In the case of adaptation to novel force fields imposed by programmable robotic devices, some studies reported asymmetries in the direction and extent of transfer (Sainburg, 2002, Criscimagna-Hemminger et al., 2003, Wang and Sainburg, 2004a, Duff and Sainburg, 2006, Schabowsky et al., 2007, Yadav and Sainburg, 2014b, Lefumat et al., 2015), while Stockinger et al. recently reported complete symmetry in transfer of adaptation to velocity dependent curl-fields imposed by a robotic device. Such forces push the arm perpendicular to the target direction (Stockinger et al., 2015). Another type of environmental perturbation that has been well-studied involves visual-motor distortions, in which visual feedback about movement is displaced or reflected. Visual displacements have been studied using physical prisms in goggles (Martin et al., 1996), while visual rotations can be imposed using computer feedback of hand position. In the case of visuomotor rotations, the computer cursor representing the hand is rotated relative to the start position of the hand, such that a straight anteriorward path of the hand will produce a straight path of the cursor that is directed a given amount (ie. 30°) relative to the hand path. Some studies of visuomotor rotation adaptation have reported that different aspects of task performance transfer asymmetrically (Taylor and Heilman, 1980, Imamizu and Shimojo, 1995, Stoddard and Vaid, 1996, Thut et al., 1996, Wang and Sainburg, 2006a, b, Anguera et al., 2007, Galea et al., 2007), while other studies have failed to verify asymmetry in transfer (Balitsky Thompson and Henriques, 2010). It should be noted that most studies that found asymmetry in transfer assessed savings, quantified as a reduction in errors when one arm is exposed to the environmental conditions that were previously adapted to with the other arm. In contrast, the studies that showed symmetry in interlimb transfer assessed after-effects, the training dependent error that is displayed when the untrained arm is exposed to a typical, null environment. These two measures likely reflect different aspects of learning and memory.

In addition to questions of whether interlimb transfer is affected by handedness, some researchers have questioned whether implicit motor learning transfers between the arms at all. Implicit learning refers to processes that are not accessible to awareness, such as conscious recognition and correction of errors. Explicit learning refers to processes that are conscious and reflect progressive corrections for perceived errors in movement (Taylor et al.,

2014). Malfait and Ostry (Malfait and Ostry, 2004, Taylor et al., 2014) provided evidence that interlimb transfer of robot induced force-fields depended on awareness of movement errors during the course of adaptation by showing that transfer is mitigated when the force environment is introduced too gradually for subjects to become aware of their movement errors. However, Wang et al. failed to corroborate those findings for a visuomotor rotation task (Wang et al., 2011). Thus, factors that appear to influence interlimb transfer of learning include the nature of the task and environmental manipulations that are introduced by the paradigm, whether errors are corrected through implicit or explicit mechanisms during adaptation, and how transfer is assessed, either by quantifying savings or aftereffects.

We designed an experiment to examine transfer of motor performance using a task that avoids the confounding factors described above. We exploit a single-joint targeted elbow movement paradigm that does not impose an environmental perturbation. Because the task is easy to perform correctly, and because participants neither receive feedback about performance nor task-accuracy, explicit information about task errors was not available during practice. In addition, previous research has shown that this task is performed symmetrically with regard to movement speed and accuracy. However, robust differences between performance with the two arms were reflected in the tangential acceleration profiles (Sainburg and Schaefer, 2004a, Yadav and Sainburg, 2011). Specifically, maximum hand velocities were scaled with movement distance in different ways for each arm. Non-dominant arm movements showed greater scaling in the duration of the initial acceleration profiles, while dominant arm movements showed greater modulation of the amplitude of the initial acceleration profiles. We previously showed that these different strategies were differentially disrupted by either left or right hemisphere damage (Schaefer et al., 2007). In short, right hemisphere lesions led to reduced scaling of acceleration duration with peak velocity, while left hemisphere lesions led to reduced scaling of acceleration amplitude with peak velocity. We concluded that these two aspects of control, scaling of acceleration peak and scaling of acceleration duration, reflect control processes that have become differentially specialized in each hemisphere.

The current study tests the specific hypothesis that asymmetry in interlimb transfer of motor performance might result from recruitment of different processes that have become specialized in each hemisphere. Thus, practice with the right arm would be expected to reinforce left hemisphere mechanisms while practice with the left arm might reinforce right hemisphere mechanisms. We expect that initial performance of our task with the right arm should reinforce scaling of acceleration amplitude with variations in peak velocity, while initial performance with the left arm should reinforce scaling of acceleration duration. We thus predict that following right arm practice, left arm performance should incorporate greater modulation of acceleration amplitude, and reduced modulation of acceleration duration, to achieve distance-dependent variations in peak velocity. In contrast, we predict that initial performance of the task with the left arm should primarily practice modulation of acceleration duration to specify scaling of peak velocity with distance, a process that should subsequently influence the right arm control strategy.

METHODS

Participants

Eleven right-handed individuals (3 males, 8 females, age 20 to 25 yr) participated in this study. Handedness was determined using a 12-item version of the Edinburgh inventory (Oldfield 1971), with all participants having a laterality quotient (LQ) of >85 . Five of the participants performed movements with their (nondominant) arm first, followed by their right (dominant) arm, while the remaining six performed movements with their right arm first followed by their left arm. Thus, this study was counter-balanced to compare left and right arm performance both under 'naïve' conditions as well as 'transfer conditions', when the unexposed arm performs the task following practice with the other arm. None of the participants had any neurological or musculoskeletal disorder affecting movements of their upper limbs. All the experiments were conducted in accordance with the Institutional Review Board of the Pennsylvania State University. A portion of this data was previously published (Sainburg, 2004). In that study, only the initial experimental session was reported (i.e., 'naïve' conditions), but interlimb transfer conditions were not included.

Participants performed experiments in a virtual reality set up illustrated in Figure 1a. They were positioned facing a projection screen with either the dominant or nondominant arm supported over a horizontal table top, positioned just below shoulder height (adjusted to each individual's comfort), by an air-jet system, which reduced the effects of gravity and friction. A cursor representing finger position, a start circle, and a target were projected on a horizontal screen positioned above the arm. A mirror, positioned parallel and below this screen, reflected the visual display, so as to give the illusion that the display was in the same horizontal plane as the fingertip. Calibration of the display ensured that this projection was veridical. All joints distal to the elbow were immobilized using an adjustable brace. This virtual reality environment ensured that participants had no visual feedback of their arm during an experimental session. Movements of the trunk and scapula were restricted using a butterfly-shaped chest restraint. Position and orientation of the segments proximal and distal of the elbow joint were sampled using a Flock of birds (FoB)[®] (Ascension-Technology, Burlington, VT) magnetic six-degree-of-freedom (6-DOF) movement-recording system, digitized at 103 Hz. Custom computer algorithms for experiment control and data analysis were written in REAL BASIC[™] (REAL Software, Inc., Austin, TX), C, and IgorPro[™] (Wavemetric, Inc., Lake Oswego, OR).

Task

The experimental task is illustrated in Figure 1b. Before all trials, the index finger position was displayed in real time as a screen cursor. The shoulder position was restrained by a brace at 20°, while the elbow angle (angle formed between upper arm and forearm) established the start and end locations of the movements. The start location was 80°, while the target locations were 90°, 100°, 115°, and 125°; thus, target positions required 10°, 20°, 35°, and 45° of elbow extension, respectively. Although target positions were individually set for each participant according to elbow angles, the average Euclidean distances were 7 cm, 13 cm, 21 cm, and 27 cm, respectively. All targets were displayed as 2.5 cm in diameter. Participants were to hold the cursor within the starting circle for 200 milliseconds, after

which time they were to move the cursor to the target using a single, uncorrected motion in response to an audiovisual “go” signal. Targets were presented in a pseudorandom order, such that no single target was presented consecutively.

Dependent Measures

Two primary metrics from the acceleration phase of movement were quantified to measure motor performance and practice effects. 1) The initial acceleration amplitude was measured as the maximum tangential acceleration achieved prior to peak velocity. 2) The acceleration duration was measured as the first time that the hand tangential acceleration profile crossed zero after the movement began (i.e. “acceleration cross-zero”), which also equals the time at which peak velocity occurred.

Normalization of acceleration profile for quantifying contribution to velocity—

In order to test our hypothesis that practice of the reaching task with either the left or the right arm will differentially affect each of these components of the acceleration profile when the task is subsequently performed with other arm, we collapsed the data across targets by removing both the time and amplitude dimensionality of the profiles. For normalized acceleration amplitude (Eq. 1), peak acceleration (A_{max}) was divided by the average acceleration of the movement, where the average acceleration was computed as hand path length (HPL) of the movement divided by the square of movement duration (t_f).

Equation 1: Normalized Acceleration Amplitude ($A_{max_{norm}}$)

$$A_{max_{norm}} = \frac{A_{max}}{HPL \times t_f^{-2}}$$

$$HPL = \sum_{i=2}^n \sqrt{(x_i - x_{i-1})^2 + (y_i - y_{i-1})^2}$$

Hand path length was computed as integral of differential path distance. Numerically, this was calculated as sum of distances between $(i-1)^{th}$ and i^{th} sample, where i varied between 2 and number of samples (n). The beginning of movement was defined by the last minima in the tangential velocity profile, prior to the peak in tangential hand velocity, that was less than 8% of peak tangential velocity.

We also normalized acceleration duration (t_{amax}) to total movement time (t_f) (Eq. 2).

Equation 2: Normalized Acceleration Duration ($Accdur_{norm}$)

$$Accdur_{norm} = \frac{t_{amax}}{t_f}$$

Because the integral of the initial acceleration profile reflects peak velocity, we were able to assess the relative contributions of these two acceleration features to velocity irrespective of target distance, once they were normalized. To do so, we calculated the ratio of normalized acceleration amplitude and normalized acceleration duration, which provides a measure of

the relative contribution of each component of the acceleration profile to velocity, across all trials and targets. For this measure, the higher the ratio, the more that acceleration amplitude contributed to velocity than did acceleration duration (Eq. 3).

Equation 3: Ratio of Normalized Acceleration Amplitude to Normalized Acceleration Duration

$$Ratio = \frac{Amax_{norm}}{Accdur_{norm}}$$

This value allowed us to directly test whether prior practice with arm affected how the other arm completed the reaching task, and whether practice effects provide support for hemisphere specific control strategies.

Statistical analysis

In order to test the primary hypothesis of this study, we needed to first ensure that peak velocities were comparable between the groups for naïve conditions. Then, we could assess the relative differences in the contributions of acceleration amplitude and duration to achieve the same velocities with the two hands. To do so, we performed a mixed factor ANOVA on mean peak velocity data with group (LR, RL) as between-subject and target (10°, 20°, 35°, and 45°) as within-subject factors. Note that for data within practice condition, such as the naïve condition alone, group is the same as hand because under naïve conditions group LR used the left hand only, and group RL used the right hand only. Based on previous data (Sainburg and Schaefer, 2004), we expected both conditions to show only a main effect of target, but no effect of arm (Group), thereby indicating comparable left and right arm peak velocities.

Because this task required familiarization, but not adaptation per se, we were interested in quantifying steady state performance. To ensure that we were in fact analyzing subjects' steady state performance, we calculated the mean coefficient of variation (CV) for peak velocity per epoch of practice. We used peak velocity to assess steady state because this was the variable that we also used to assess the two different control strategies that were measured as modulation of acceleration amplitude and modulation of acceleration duration, respectively. In addition, under naïve conditions, peak velocities were similar between the hands, as described above. Each session (naïve, and transfer) consisted of 150 trials, separated into 15 epochs of 10 trials. While targets were presented randomly, each epoch consisted of at least 2 trials to each target. The two groups (RL and LR) either performed the task with the right hand first (RL), prior to performing with the left hand, or vice versa (LR). The two conditions were either the first session of each group, in which the participant performed under Naïve Performance (NP) conditions, without prior exposure to the task, or under the Transfer Condition (TR), referring to the second session that followed Naïve performance. We ran a 2 (Group: RL, LR) × 2 (Practice Condition: Naïve NP, Transfer Condition TR) × 15 (Epoch) mixed factor ANOVA. We confirmed that subjects were in fact in steady-state by a 2 (Group: RL, LR) × 2 (Practice Condition: Naïve NP, Transfer Condition TR) × 10 (Epoch) mixed factor ANOVA, for the last 10 epochs, or 100 trials. We

then collapsed each dependent variable across the remaining 10 epochs (100 trials) for further analysis.

Our primary predictions for this study were based on pairwise analysis of normalized acceleration amplitude, normalized acceleration duration, and the ratio between these values. Again, these values were calculated according to Equations 1, 2, and 3, respectively (see above). For pairwise analysis and for post-hoc pairwise analysis of data subjected to the ANOVA analysis described above, we performed student's *t* tests.

RESULTS

Steady State Performance

Figure 2 shows the coefficient of variation in peak velocity for both the left and right arms across both practice conditions (Naïve performance -NP and Transfer - TR). Each data point shows the average ($\pm$ SE) of every 10 trials, or one epoch. As described above, we used peak velocity to identify steady state performance because this is the aspect of performance most directly affected by our two dependent measures and because under naïve conditions, this variable is not significantly different between the arms. For both left and right arms of both groups, the coefficient of variation was highest in the early epochs, as reflected by a main effect of epoch in our mixed factor ANOVA for the first five epochs ($F(1,9) = 50.15$, $p < 0.0001$). Importantly, the effect of epoch was no longer significant ($F(1,9) = 2.28$, $p = 0.166$) after the first five epochs, indicating that subjects had reached a 'steady state' of performance. We note that the relatively high coefficient of variation (30–40%) in the steady state reflects target-dependent variations in velocity, as intended by our experimental design (see Fig 1). The remaining results below describe differences in arm and practice effects observed during this steady state phase.

Naïve Performance: Interlimb Differences in Control Strategy

Sample hand paths (Fig. 3A) and their corresponding tangential hand velocity profiles (Fig. 3B, black traces) to each of the four targets are shown for an individual subject. Note the systematic increase in peak velocity with target distance for both arms and that movement time has been normalized (0% = start; 100% = end). Figure 3B also shows the average ($\pm$ SE) peak velocities as bars across subjects for the four targets along the left-wall (i.e. z-axis) of the graphs, which are consistent with the trends in peak velocity observed in the individual subject's traces. Importantly, these data are shown for the naïve condition. As expected, there was a main effect of Target ($F(1,9) = 403.87$, $p < 0.0001$) but no main effect of Arm ($F(1,9) = 0.036$, $p = 0.855$) on peak velocity for the naïve condition, confirming that both arms showed similar velocities that scaled across movement distances. In addition, there were no differences in final position errors between arms ($F(1,9) = 0.299$, $p = 0.597$), but there was a main effect of target ($F(1,9) = 7.087$, $p = 0.026$).

Figure 4A shows the tangential hand acceleration profiles that correspond to the individual hand paths and tangential velocity profiles in Figure 3. The left-wall of each graph in Figure 4A shows the average ($\pm$ SE) peak acceleration for each target across subjects. Note that although *within* each arm, the acceleration profiles scaled systematically with target

distance, *between* the arms the profile shapes are markedly different. As described in the Methods, the time at which tangential hand acceleration becomes negative (“acceleration cross-zero”) indicates the timing of peak hand velocity. This important variable captures the acceleration duration, and is represented as an open circle on each acceleration profile in Figure 4A, thereby illustrating changes (or lack thereof) in acceleration duration across target distances and between arms. For peak acceleration, we observed main effects of both target ($F(1,9) = 64.86$, $p = 0.0001$) and arm ($F(1,9) = 12.83$, $p = 0.0059$), as well as an interaction between target and arm ($F(1,9) = 7.770$, $p = 0.021$). For acceleration duration, our ANOVA revealed a main effect for both target ($F(1,9) = 44.01$, $p < 0.0001$) and arm ($F(1,9) = 12.70$, $p = 0.006$). As evident in Figure 4, these patterns depended on the arm, such that peak accelerations were greatest for the right arm ($t(9) = 3.58$, $p = 0.006$), while acceleration durations were greatest for the left arm ($t(9) = -3.56$, $p = 0.006$). In other words, both arms achieved similar peak velocities using different strategies: While the dominant-right arm peak accelerations were large relative to the non-dominant-left arm, right arm acceleration durations were relatively small. The left arm generated smaller accelerations over larger durations to achieve similar peak velocities.

By normalizing acceleration amplitude to the average acceleration of each trial, and normalizing time to movement duration, we were able to collapse the data across targets. Figure 5A shows the average normalized acceleration amplitude (right axis) and duration of acceleration (left axis) for the left and right arms. This analysis emphasizes the large strategic differences in left and right arm movements, under naïve conditions. The left arm generated lower accelerations than the right arm ($t = -8.02$, $p < 0.0001$) over longer durations than the right arm ($t = 6.76$, $p < 0.0001$), regardless of target amplitude.

In order to develop a single measurement of these two different strategies, we took the ratio of normalized acceleration amplitude to normalized acceleration duration. As shown in Figure 6B, this measure was substantially smaller for the left arm than the right arm ($t = 6.12$, $p = 0.0002$). Because this value reflects the difference in acceleration profile shape between the two arms, we exploited this single measure to assess interlimb transfer.

Interlimb Transfer: Changes in Interlimb Differences in Control Strategy

Figure 6C shows the ratio of acceleration amplitude and duration for the left and right arms under naïve performance and transfer conditions, following practice with the other arm. The substantial interlimb differences in control strategy under naïve conditions were ‘washed out’ by previous practice with the other arm, such that there were no longer statistical differences in the ratios for the left and right arms. This effect was confirmed by the interaction between condition (Naïve vs. Transfer) and Group (RL vs. LR) ($F(1,9) = 42.519$, $p = 0.045$). Post hoc analysis revealed a significant difference in this measure under naïve conditions ($t(9) = 6.120$, $p = .0002$), but not after practice with the other arm ($t(9) = -1.855$, $p = 0.096$). Thus, substantial transfer of control strategy occurred after a small amount of practice in this simple single-joint task that does not require any adaptation to visuomotor or mechanical perturbations.

DISCUSSION

The current study was designed to test the hypothesis that interlimb transfer in performance of a motor task might depend upon recruitment of processes that are specialized to the hemisphere that is contralateral to the arm that first practiced the task. We exploited a well-characterized task that does not impose visuomotor or dynamic perturbations, and that has been shown to rely on each hemisphere for different aspects of control (Sainburg and Schaefer, 2004b, Schaefer et al., 2007). We predicted that initial performance of the task with the right arm should practice left hemisphere acceleration amplitude scaling mechanisms, and initial practice with the left arm should practice right hemisphere acceleration duration scaling. Our findings indicate substantial transfer of control strategy between the arms. Because previous research has associated each control strategy with different hemispheres (Schaefer et al., 2007), our current findings suggest that hemispheric specialization for different motor control mechanisms influence the quality of interlimb transfer.

Control of Unilateral Movements Depends on Both Hemispheres

One fallacy that can easily be made regarding hemispheric asymmetry for motor control is that symmetric activation of the hemispheres reflects symmetric representation of motor control processes. However, due to the inherent cross-hemispheric anatomy of sensorimotor systems, elegantly explicated by Kuypers and colleagues (Kuypers, 1982), one should conclude that hemispheric symmetry in motor control should only require contralateral hemisphere recruitment. That is, during right arm control, there would be no reason to recruit the right hemisphere because both hemispheres would be expected to contain identical control circuits. By logical extension, bi-hemispheric activation profiles during planning and control of unilateral movements should reflect asymmetry of motor control processes. In fact, bilateral recruitment, although rarely symmetric in nature, seems to be the rule for unilateral movements (Kim et al., 1993, Kawashima et al., 1994, Remy et al., 1994, Wassermann et al., 1994, Singh et al., 1998a, Singh et al., 1998b, Nirkko et al., 2001, Kobayashi et al., 2003, Verstynen et al., 2005, Ghacibeh et al., 2007, Kicic et al., 2008, van Wijk et al., 2012, Derosiere et al., 2014). Both hemispheres are recruited for even very distal movements of either hand, while movements of the non-dominant arm and hand appear to recruit the ipsilateral hemisphere motor related areas to a greater extent than do dominant arm movements (Kawashima et al., 1993, Li et al., 1996). It is not known whether this asymmetry in recruitment is related to the tasks used in these studies, but in support of this, some studies have reported greater ipsilateral recruitment during more “complex” tasks (Chen et al., 1997).

A strong prediction of this bilateral-hemisphere motor control hypothesis is that lesions to motor related areas in one hemisphere should produce hemisphere specific motor deficits in the ipsilesional arm, the arm on the same side of the body as the hemisphere that has the lesion. In patients with middle cerebral artery lesions, this would refer to the non-paretic arm. In fact, ipsilesional arm motor deficits have been reported in the literature as early as 1967 (Wyke, 1967), and the hemisphere-specificity of these deficits was revealed over many studies and laboratories using detailed kinematic and kinetic analysis (Hermsdorfer et al.,

1999a, Hermsdorfer et al., 1999b, Haaland et al., 2004, Yarosh et al., 2004, Wetter et al., 2005, Schaefer et al., 2007, Chestnut and Haaland, 2008, Haaland et al., 2009, Poole et al., 2009, Schaefer et al., 2009b, a). The laboratories of Winstein (Pohl et al., 1996, Pohl and Winstein, 1999, Winstein et al., 1999, Stewart et al., 2014b, a) and Haaland (Haaland and Harrington, 1989, Harrington and Haaland, 1991, Haaland and Harrington, 1994, 1996) corroborated findings that left-hemisphere lesions produce deficits in the early acceleration phase of motion, but not in the late deceleration phase. Recognizing that early movement parameters reflected predictive or planned aspects of control while later phases incorporated error corrections, these authors proposed the idea that the left-hemisphere mediates open-looped control mechanisms, consistent with Liepmann's (Liepmann, 1905, Geschwind, 1975) proposal of left-hemisphere dominance for motor programming. However, they also proposed that the right hemisphere was specialized for closed-loop control. The generality of this hypothesis for the visual modality failed to be confirmed by studies that manipulated visual feedback during movements of each arm (Haaland et al., 2004).

Studies that examined detailed kinematic and kinetic variables suggested a modification of the open-closed loop hypothesis: These studies proposed that the left-hemisphere is specialized for control of predictable features of movement through largely feedforward mechanisms, including coordination of intersegmental and environmental dynamics to specify optimal movement trajectories that are lower in energetic as well as trajectory costs (Schaefer et al., 2012, Mani et al., 2013, Mutha et al., 2013). In contrast, the right hemisphere is specialized for dealing with unpredictable circumstances through modulation of limb impedance, incorporating feedback control, but modulated through feedforward control mechanisms (Yadav and Sainburg, 2014a, b). This hypothesis is consistent with a larger and more extensive theoretical framework, based on studies in a wide range of vertebrae species, proposed by MacNeilage and Rogers (MacNeilage et al., 2009). According to this idea, the left-hemisphere is specialized for specifying behavior under predictable environmental circumstances, while the right hemisphere is specialized for responding to unanticipated changes in the environment. Our hypothesis of predictive and impedance control reflects the mechanical analog of this framework. The idea that both hemispheres are recruited for unilateral movements is consistent with our current findings that indicate interlimb transfer following unilateral practice. Previous practice with one arm led to greater incorporation of that arm's control strategy during subsequent performance with the other arm: increased contribution of acceleration amplitude to peak velocity following right arm practice and increased contribution of acceleration duration to peak velocity following left arm practice.

Hemispheric Specialization for Controlling Movement Distance

This bi-hemispheric model of motor control has previously been examined using the single joint paradigm presented in the current paper. A great deal of previous work on single-joint movements directed toward targets of varied amplitude has shown that acceleration amplitude (Sainburg and Schaefer, 2004b, Mutha and Sainburg, 2007), initial EMG peak amplitude (Corcos et al., 1989, Gottlieb et al., 1989, Gottlieb et al., 1990) or the initial amplitude of the time derivative of a force pulse (Ghez and Gordon, 1987, Gordon and Ghez, 1987a, 1987b) is specified prior to movement. In contrast, acceleration duration is

modulated during the course of motion to correct for improperly specified amplitudes (Brown and Cooke, 1990, Cooke and Brown, 1990, Gottlieb, 1996, Mutha and Sainburg, 2007). In order to understand these control processes in more detail, Yadav and Sainburg (Yadav and Sainburg, 2011, 2014a) conducted simulations that combined two controllers in sequence: a predictive controller and an impedance controller. The predictive controller specified optimal trajectories, based on kinetic and trajectory costs, while the impedance controller specified stiffness and viscosity parameters in accord with a desired final position, similar in nature to equilibrium point control (Flash, 1989, Latash and G.L., 1990, Latash and Gottlieb, 1991). When this controller was fit to trajectories from healthy young participants, the predictive controller persisted longer for dominant-arm movements, while the impedance controller was initiated only at the very end of the movement to stabilize the final position. In contrast, for non-dominant arm movements, the predictive controller functioned to initiate the movements, while the impedance controller took over in the very early phase of motion near the time of peak tangential hand acceleration. In fact, for the single joint paradigm used in the current study, the acceleration amplitude modulation of the dominant arm was controlled through the predictive controller and acceleration duration modulation emerged as a result of impedance control.

In a previous study, we asked whether each of these aspects of control might be mediated by different hemispheres. Two groups of patients, one group with left hemisphere damage (LHD) and another group with right hemisphere damage (RHD) were matched for lesion volume and location and were compared with age and gender matched control participants. All groups performed the single elbow-joint reaching paradigm used in the current study. Our findings indicated that LHD produced ipsilesional deficits in modulation of acceleration amplitude, while RHD produced ipsilesional deficits in modulation of acceleration duration (Schaefer et al., 2007). In combination with our simulation studies, these findings suggest that left hemisphere mechanisms modulate acceleration amplitude, while right hemisphere mechanisms modulate acceleration duration, which reflect predictive and impedance control strategies, respectively.

Our current findings are consistent with this conclusion: Initial practice with the right arm reinforced left-hemisphere predictive control mechanisms that appear to mediate acceleration amplitude modulation. Following this practice, left arm movements showed increased contributions of peak acceleration to peak velocity. We interpret this as reflecting improved reliance on predictive control mechanisms. Initial practice with the left arm led to reinforcement of right-hemisphere impedance control mechanisms, which subsequently increased the contribution of acceleration duration to peak velocity during right arm movements. Interlimb transfer thus seemed to depend on the degree to which the previous practice with the other arm recruited hemisphere specific control mechanisms (Schaefer et al., 2007).

However, it should be noted that this asymmetry in transfer seems somewhat discrepant with the idea of bihemispheric control. That is, if practice with the dominant-right arm recruits both predictive mechanisms from the left hemisphere and impedance mechanisms from the right hemisphere, why doesn't this practice reinforce both mechanisms? Our previously described simulation studies might offer an explanation for this (Yadav and Sainburg, 2011,

2014a). In those studies, the specific mechanism that reflected contralateral hemisphere control (ie. Predictive control for left-hemisphere/right-arm and impedance control for right-hemisphere/left-arm), dominated control for most of the movement. Thus, practice with the dominant-right arm would be expected to practice left-hemisphere control to a greater degree than right hemisphere control mechanisms and vice versa. Following practice with the right arm, the major change in left-arm control reflected predictive mechanisms (ie-peak acceleration modulation), and following practice with the left arm, the major change in right-arm control reflected impedance mechanisms (ie – acceleration duration mechanisms). We thus suggest that the asymmetry in transfer arises from asymmetry in recruitment of each hemisphere during initial practice, with the contralateral hemisphere being recruited to a greater extent during practice than the ipsilateral hemisphere.

A striking difference between previous findings of transfer of visuomotor rotation adaptation (Sainburg and Wang, 2002a, Wang and Sainburg, 2004b, 2006b, a, Galea et al., 2007, Chase and Seidler, 2008) and the current findings for transfer of control strategies during a simple single joint task is that in the former studies, predictive control of direction transferred from the left arm to the right arm in right-handers. In the current study, initial practice of the task with the right arm led to increased reliance on acceleration amplitude, reflecting predictive control mechanisms. Similarly, in previous studies of visuomotor rotation adaptation, final position accuracy transferred from initial adaptation with the right arm to left arm adaptation. For adaptation to visuomotor adaptation tasks, the processes associated with the ipsilateral hemisphere during initial adaptation were transferred to the other arm to yield savings during subsequent adaptation. In the current study, the processes associated with the *contralateral* hemisphere during initial practice were transferred to the other arm. While both studies show asymmetric transfer of lateralized aspects of motor control, the direction of transfer of the associated performance variables appear to be oppositely directed. We expect that these differences between findings might be due to the degree to which ipsilateral hemisphere processes are stressed during initial practice. For adaptation to novel visuomotor rotations, it is critical for left arm movements to recruit left-hemisphere direction control processes. In support of this, left arm direction adaptation to visuomotor rotations is completely disrupted by left, but not right posterior parietal lesions (Mutha et al., 2011, Mutha et al., 2014). In addition, for right arm adaptation, final position corrections during adaptation depend on right hemisphere mechanisms, as reflected by the fact that such corrections are disrupted by lesions to right, but not left, posterior prefrontal cortex regions. Therefore, visuomotor rotation adaptation appears to require recruitment of ipsilateral cortex mechanisms (Clower et al., 1996, Chase and Seidler, 2008). In contrast, the current single joint study was practiced without a requirement to modify performance in accord with variables that reflect ipsilateral hemisphere mechanisms. The transferred variables, instead, reflect after-effects in the acceleration profile that seem to be largely mediated by contralateral hemisphere. The difference seems to be that during initial practice of this task, specification of velocity scaling is largely determined by each arm's contralateral hemisphere mechanisms: The right arm exploits scaling of acceleration amplitude, a process that is disrupted by left-hemisphere lesions, while the left arm scales peak velocity with distance by modulating acceleration duration, a process disrupted by right-hemisphere lesions. Because this task does not require nor stress a requirement to increase the role of

ipsilateral hemisphere mechanisms during initial practice, practiced contralateral hemisphere mechanisms are reflected as ‘aftereffects’ in the unpracticed arm. Further research is necessary to test this hypothesis that may help explain apparent discrepancies between the direction of transfer between previous studies of visuomotor rotations and our current findings.

Our theoretical interpretation of the current findings is based on the idea that each hemisphere has become specialized for different aspects of motor control. This hypothesis is consistent with lesion studies that have shown that right and left hemisphere lesions produce different motor control deficits in the ipsilesional arm of stroke survivors (Hermsdorfer et al., 1999a, Hermsdorfer et al., 1999b, Haaland et al., 2004, Yarosh et al., 2004, Wetter et al., 2005, Schaefer et al., 2007, Chestnut and Haaland, 2008, Haaland et al., 2009, Poole et al., 2009, Schaefer et al., 2009b, a). However, it is also plausible that each hemisphere mediates similar control mechanisms, but that each hemisphere has become more practiced in one or the other mode of control, leading to different control strategies under naïve conditions. Our current results indicate that after practice with either arm, transfer results in more symmetrical behavior, reflected in the contributions of acceleration amplitude and duration to peak velocity (see figure 5b). It is plausible that this change toward more symmetrical behavior between the arms might not be due to differential training of one or the other hemisphere, but might instead result from a general training effect on both mechanisms in each hemisphere. This hypothesis would predict that single limb training should result in a similar change in strategy with time, an effect that we did not see in the current data. This may be due to the fact that we did not vary the amount of training that individuals experienced, prior to transfer. It should be noted that Lei and Wang (Lei and Wang, 2014) recently varied the amount of training of the left arm in a visuomotor rotation task from 160 to 320 to 400 trials, but showed no effects on the extent of interlimb transfer of this training. Nevertheless, in the current study, it is not clear whether more training with one arm might have led to the changes in strategy that were noted following transfer to the other arm. Further research is needed to evaluate this prediction.

Dependence of interlimb transfer on Handedness

In this study, all of our subjects were strongly right-handed (LQ >85). However, our results suggest that interlimb transfer depends on lateralized motor control processes. Because handedness, in turn, emerges from hemispheric lateralization of motor control processes (Yadav and Sainburg, 2014a), we conclude that asymmetry in interlimb transfer is affected by hemispheric lateralization for motor control. Two previous studies have demonstrated that the extent of interlimb transfer of novel dynamic conditions (Lefumat et al., 2015) as well as visuomotor rotations and sequence learning (Chase and Seidler, 2008) depends on an individual’s laterality quotient, which presumably reflects both the direction and extent of handedness. In the latter study, the extent of transfer was greater for subjects who were less-handed (lower LQ). The authors interpreted these findings from the point of view that transfer might be determined by the degree to which ipsilateral hemisphere is recruited during initial learning. They pointed out that individuals with lower laterality quotients have enlarged corpus callosum (Witelson, 1985, Witelson and Goldsmith, 1991) and that less strongly lateralized individuals tend to recruit ipsilateral motor cortex to a greater extent than

those who are more behaviorally lateralized (Dassonville et al., 1997). From this point of view, the extent of interlimb transfer depends on the degree to which the task in question recruits ipsilateral hemisphere, which may depend on the degree of motor lateralization of the individual. However, Lefumat et al (2015) showed that transfer of dynamic learning is reduced in individuals with lower LQ. The discrepancy between these two studies may have to do with the differences in how individuals adapt to dynamic versus visual-motor distortions. In fact, the nature of the adaptation environment, as well as the extent of initial error information has previously been shown to greatly influence the amount and symmetry of initial learning, which in turn influences potential for transfer (Duff and Sainburg, 2006, Schabowsky et al., 2007). In our current study, no environmental perturbation was introduced. Our findings suggest that asymmetry in transfer is related to asymmetry in hemispheric specializations for different aspects of motor control. It remains to be determined whether transfer in this task may also depend on the direction and extent of handedness, a question that could not be addressed here because our participants were selected based on a laterality quotient of +85 or greater.

Conclusions

This study was designed to test whether practice of a single joint targeted reaching task with one arm will transfer to affect reaching performance with the other arm. This single elbow joint task performed without visual feedback was chosen because previous research had indicated that right-handed participants perform this task symmetrically with regard to peak hand velocity and task accuracy, but asymmetrically with regard to the underlying control strategies reflected in the acceleration profiles. While both right-dominant and left-non-dominant arms scale peak hand velocities with movement distance, this is achieved systematically differently with each arm. While the right arm scales acceleration amplitude, the left arm maintains fairly constant amplitudes, instead scaling acceleration duration to achieve different velocities. Most importantly, these two strategies have been shown to depend on left and right hemisphere mechanisms through studies in stroke patients with left and right hemisphere damage (Schaefer et al., 2007). In the current study, we exploited this task in order to ask whether potential transfer effects between the arms might depend on these hemisphere specific control strategies. Our findings confirmed this hypothesis by indicating that previous practice with the right arm transferred to the left arm, such that the left arm showed greater dependence on acceleration amplitude modulation to achieve variations in peak velocity. Similarly, previous practice with the left arm transferred to the right arm, resulting in greater dependence on acceleration duration modulation to achieve variations in peak velocity. These findings indicate that interlimb transfer resulted in greater symmetry in performance between groups, using either the right or left arm. These findings suggest that hemispheric specialization for different motor control mechanisms influence the quality of interlimb transfer. We postulate that transfer of hemisphere-specific control mechanisms results from bihemispheric control of reaching. Studies in right-handed stroke patients with right and left damage have confirmed that, in this task, acceleration amplitude modulation is mediated by left hemisphere mechanisms and thus disrupted by left hemisphere damage. In contrast, acceleration duration modulation is mediated by right hemisphere mechanisms and thus disrupted by right hemisphere damage (Schaefer et al., 2007). Importantly, these hemisphere specific deficits in each control mechanism were

observed in the ipsilesional arm of stroke patients, indicating a role of the ipsilateral hemisphere in this task. While these findings indicate a role of both hemispheres in control, we suggest that a greater dependence of each arm on the control strategy associated with its contralateral hemisphere leads to practice effects that preferentially train contralateral hemisphere mechanisms during practice. As a result, transfer to the opposite arm results in a greater influence on the strategy associated with the hemisphere contralateral to the previously trained arm. Thus left arm practice transferred to increase reliance on acceleration duration modulation in the right arm, and right arm practice transferred to increase reliance on acceleration amplitude modulation in the left arm. Finally, the fact that these aspects of performance readily transfer across the arms, but do not impose asymmetries on the speed or accuracy of movements, suggest that this aspect of transfer is implicit, supporting the idea that interlimb transfer of motor learning is not wholly dependent on explicit mechanisms.

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Highlights

1. Hypothesis: Asymmetry of interlimb transfer depends on Hemispheric Specialization.
2. Tested single joint targeted elbow movements to different distance targets.
3. Acceleration amplitude modulation transferred to non-dominant left-arm.
4. Acceleration duration modulation transferred to dominant right-arm.
5. Conclusion: Interlimb transfer depends on lateralized motor control processes.

Figure 1.

Figure 1a – Experimental Set-up. Participants were positioned facing a horizontally positioned mirror that reflected the 55" monitor. The dominant or nondominant arm was supported over a table top by an air-jet system, which reduced the effects of gravity and friction. All joints distal to the elbow were immobilized using an adjustable brace, and the upper arm was immobilized by a brace attached to the table. Figure 1b - Experimental Task. Prior to each trial, participants viewed a cursor that represented the forefinger-tip, in order to position the cursor within the start circle. After 200 milliseconds in the start circle, a go tone was given and the cursor disappeared. Targets were calibrated to each participant's forearm dimensions, such that the targets required 10, 20, 35, and 45 degrees of elbow extension, respectively.

Figure 2.

(Mean $\pm$ SE) Coefficient of variation of peak velocity for both the left and right arms across both task conditions: Naïve and Transfer (TR). Each data point shows the average ($\pm$ SE) of every 10 trials, or one epoch. Epochs 6–15 reflect the steady state phase of performance.

Figure 3. Sample hand paths (Fig. 3A) and corresponding tangential hand velocity profiles (Fig. 3B) for each target. Figure 3B shows the average ($\pm$ SE) peak velocities as bars across subjects for the four targets along the left-wall (i.e. z-axis) of the graphs.

Figure 4.

Figure 4A - Tangential hand acceleration profiles that correspond to the individual hand paths and tangential velocity profiles in Figure 3. The white circles indicate the acceleration cross-zero point for each profile. Figure 4B - average $\pm$ SE for acceleration cross-zero, measured in percentage of movement time, across all subjects for each target.

Figure 5.

Figure 5A - Average normalized acceleration amplitude (right axis) and duration of acceleration (left axis) for the left and right arms. Figure 5B - ratio of normalized acceleration amplitude to normalized acceleration duration, across all subjects. Figure 5C - ratio of acceleration amplitude and duration for the left and right arms under naïve conditions and transfer conditions.