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Handedness can be explained by a serial hybrid control scheme

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Abstract

Our previous studies in healthy individuals and stroke patients led us to propose that the dominant and nondominant arms are specialized for distinct motor control processes. We hypothesize that the dominant arm is specialized for predictive control of limb dynamics, and the nondominant arm is specialized for impedance control. We previously introduced a hybrid control scheme to explain lateralization of single-joint elbow movements. In this paper we apply a similar computational framework to explore interlimb differences in multi-joint reaching movements: the movements of both arms are initiated using predictive control mechanisms, and terminated using impedance mechanisms. Four parameters characterize predictive mechanisms, four parameters characterize impedance mechanisms, and a 9th parameter describes the instant of switch between the two modes of control. Based on our hypothesis of motor lateralization, we predict an early switch to impedance control for the nondominant arm, but a late switch, near the end of motion, for the dominant arm. We fit our model to multijoint reaching movements of each arm, made in the horizontal plane. Our results reveal that the more curved trajectories of the nondominant arm are characterized by an early switch to impedance mechanisms, in the initial phase of motion near peak velocity. In contrast, the trajectories of the dominant arm were best fit, when the switch to impedance mechanisms occurred late in the deceleration phase of motion. These results support a model of motor lateralization in which the dominant controller is specialized for predictive control of task dynamics, while the nondominant arm is specialized for impedance control mechanisms. For the first time, we are able to operationally define handedness expressed during multi-joint movements by applying a computational control model.

Keywords

Motor Lateralization; Handedness; Dynamic Dominance; Motor Control; Predictive Control; Impedance Control

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Introduction

Lateralization is a basic organizational feature of the nervous system that is reflected in the fact that during the course of evolution the relative size of the corpus callosum and anterior commissure has decreased while the size of intrahemispheric circuitry has increased (Rilling and Insel, 1999; Herculano-Houzel, 2010). These relative changes reflect the evolutionary emergence of new processes that are represented by local circuits in one or the other hemisphere. As such circuits are distributed between the hemispheres, the corpus callosum becomes a conduit for output from these circuits, rather than serving a primary role in neural computations. Thus, as new neurobehavioral functions arise during evolution, such as language, cognitive processes, and complex and coordinated arm movements, they are represented by local, lateralized circuitry. The selective pressure to localize functions to circuits within a single hemisphere is probably related to reduction of both energetic and time costs associated with neural processing (Aboitiz et al., 2005). In addition, some lateralizations, such as visual perceptual processes in avians have been shown to be critical for efficient performance of two different tasks in parallel, when those tasks require specialized processes in different hemispheres (Rogers, 2012; Rogers et al. 2013). Lateralizing distinct competitive functions to different hemispheres compartmentalizes the corresponding neural mechanisms, and preserves their neural integrity and fidelity. In humans, many lateralized processes including visual information processing, cognitive, memory, and language functions have been delineated through the foundational split-brain research of Sperry and Gazzaniga (Bogen et al, 1969 Sperry 1961, Gazzaniga, 1998, 2000). However, such neural organization of motor functions is less well understood.

Neural lateralization of motor control processes is apparent through the everyday experience of handedness, the tendency to prefer the ‘dominant’ arm for performance of many everyday unilateral tasks, such writing, using scissors, and throwing a ball. Handedness has also been described as an asymmetry in the time and/or accuracy associated with fine motor tasks (Annett et al. 1979; Carson 1993; Carson et al. 1990; Sainburg, 2005; Sainburg and Kalakanis, 2000). We have recently linked these two manifestations of handedness: We showed that hand preference changes for reaching to different locations in space can reverse, depending on which hand has the accuracy advantage (Przbyla et al, 2013). Thus, when reaching to a large number of targets across the workspace, certain locations show dominant arm advantages when subjects have visual feedback and nondominant arm advantages when reaching without visual feedback. Subjects readily switch arms to these locations when reaching under the different feedback conditions. Regardless of previous success in defining handedness by preference and/or performance asymmetries, the underlying neural and control-based processes that drive these asymmetries remain largely unknown.

We have postulated that motor lateralization reflects the specialization of each arm-hemisphere system for distinct and complimentary control processes (Sainburg, 2010). According to this idea, each brain hemisphere contributes unique control mechanisms to the control of both arms, reflecting bi-hemispheric control of each arm. We propose that the dominant arm-hemisphere system is specialized for optimizing dynamic aspects of movement related to the direction and shape of the movement trajectory, and associated energetic costs (Bagesteiro and Sainburg, 2002; Mutha et al., 2011; Sainburg, 2002;

Sainburg and Kalakanis, 2000; Schaefer et al., 2007, 2009a). This leads to advantages for this arm in specifying trajectories for throwing projectiles, drawing, and rapid reaching. Such control is based largely on predictive mechanisms that anticipate and account for the dynamic properties of the arm and the task environment. The hemisphere contralateral to the non-dominant arm is, instead, specialized for impeding forces and achieving stable postures, or stable “equilibrium” positions (Bagesteiro and Sainburg, 2003; Duff and Sainburg, 2007; Wang and Sainburg, 2007), leading to advantages in stabilizing objects such as bread, nails, and tools that are being cut, hammered or shaped by the dominant arm. As a result, the non-dominant arm often shows better accuracy and precision in achieving a desired spatial position, particularly when an ongoing movement is perturbed (Bagesteiro and Sainburg, 2003; Duff and Sainburg, 2007), or when performing in the absence of visual feedback (Przybyla et al., 2013). We suggest that these two mechanisms are exploited for control of each arm, but that the contralateral arm enjoys greater influence of its controller due to direct sensorimotor connections.

Our bihemisphere motor lateralization hypothesis has direct predictions for patients with unilateral brain lesions due to stroke. First, patients should exhibit ipsilesional deficits in the non-paretic arm and these deficits should be hemisphere specific. We have verified this prediction in a series of previous studies of reaching movements that have documented deficits in final position stabilization and accuracy in patients with right hemisphere damage (RHD), but sparing of intersegmental coordination and trajectory straightness. In contrast, patients with left hemisphere damage (LHD) show deficits in intersegmental coordination and trajectory, while demonstrating accurate final position control (Schaefer et al., 2007, 2009a). Such findings verify that when patients lose the contributions from ipsilateral hemisphere, they show specific deficits associated with that hemisphere’s control specialization, but sparing of the other hemisphere’s specialized processes. We have recently shown that in patients with mild paresis, the same hemisphere specific deficits are evident in the contralesional, slightly paretic arms of stroke patients (Mani et al, 2013). Thus, our bihemispheric model of motor lateralization has been supported by previous studies in healthy young subjects and patients with unilateral hemisphere damage.

The purpose of the current study is to examine whether the different coordination patterns exhibited during dominant and nondominant arm reaching could be attributed to different contributions of each type of control. We postulate that right arm trajectories that are fairly straight and smooth result from a predominant influence from predictive control of dynamics, while the more curved profiles of the nondominant arm reflect mechanisms dominated by impedance control processes. We have previously demonstrated that interlimb differences in single joint movement accelerations could be described by differential contributions from both types of controllers (Yadav and Sainburg, 2011). However, that study did not address the trajectory differences observed during multijoint movements. We now formalized our hypothesis into a computational model that describes movement control through a hybrid scheme where predictive mechanisms are used to initiate movements, and impedance mechanisms to terminate movements. The switch of control to the impedance mechanism can happen any time after movement initiation. By fitting our model to empirically derived reaching movements with the dominant and non-dominant arms, we can ask whether such a control scheme would yield systematic differences in reliance on each

type of controller, and whether these differences reflect the specializations predicted by bihemispheric model of motor lateralization.

Methods

Subjects

A total of 6 healthy right-handed young adults (3-Males, 3-Females) between the ages of 18–25 were recruited from the college community. Handedness was assessed using a modified version of Eidenburg inventory (Oldfield, 1971). All the subjects signed an informed consent form approved by the institutional review board of the Pennsylvania State University.

Experimental apparatus

The experimental apparatus is presented in Figure 1. The subjects sat facing a table with their arms supported on air-sleds. Subjects were presented with 2-D virtual reality environment by a mirror that reflected an LCD screen, positioned horizontally and above the mirror. A cursor placed at the subject's fingertip was displayed in the screen. Subjects were instructed to move this cursor from a start position to a target in response to a 'go' signal. After movement initiation, the cursor disappeared, and the subjects did not receive feedback about the position of their finger during the trial. At the end of the trial, a circle placed at the final position provided accuracy feedback. Subjects were instructed to move faster than 0.8 m/s. Points were given based on how close the finger got to the target, but only on trials with a maximum velocity above 0.8 m/s. A flock of birds (FOB: Ascension-Technology), electromagnetic 6-degree of freedom position and orientation tracking system was used to record movements of the shoulder, elbow, wrist and fingertip at 130 Hz. Custom data analysis code was written in REALBASIC (REAL Software, Inc.), IgorPro (Wavemetric, Inc) and MATLAB (Mathworks, Inc).

Experimental protocol

Subjects performed 150 reaching movements from a start position (elbow: 90°, shoulder: 25°) to 3 20 cm targets, directed 50°, 90°, and 130°, relative to the frontal plane. The targets were presented in a pseudo-randomized order. Half of the subjects performed 75 reaching movements with their dominant arm followed by the nondominant arm. The other half performed movements with the nondominant arm first. In our previous studies, we showed consistent differences between the limbs, whether we used a within subject design, alternating between the limbs every few trials (Sainburg and Kalakanis, 2000) or a between subjects design, in which each group of subjects used either the left or right arm in a block of trials (Bagesteiro and Sainburg, 2002; 2003). Here, we employ a within subjects design. Due to the potential for interlimb transfer (Sainburg and Wang, 2002) to produce an order-effect, we counterbalance the order of the right and left arm blocks of trials between subjects. We analyzed the last 48 trials of each arm to allow for task familiarization. We first synchronized movements toward each target by matching the instant of peak acceleration. We then computed an average trajectory toward each target from all the 16 trials toward each target. We then fit our controller to this average trajectory.

Numerical methods

Hybrid control model—We extend the computational model proposed in Yadav and Sainburg, 2011 to multi-joint movements. According to our computational model of control, movements are initiated using predictive mechanisms, and terminated using impedance mechanisms. We propose that the predictive mechanisms seek to minimize a cost of movement that combines the error from the desired end state, and implicit energetic costs of movements. We define this cost function as,

$$Cost = \int_0^{t_f} \left(\left| \tau_s \dot{\theta}_s \right| + \left| \tau_e \dot{\theta}_e \right| + (\Theta - \Theta_f) Q_{\Theta} (\Theta - \Theta_f) + (\dot{\Theta} - \dot{\Theta}_f) Q_{\dot{\Theta}} (\dot{\Theta} - \dot{\Theta}_f) \right) dt \quad (1)$$

where t_f is the movement time, τ is the joint torque, $\dot{\theta}$ is the joint velocity, and subscripts 's' and 'e' represent shoulder and elbow. Θ is the vector of joint angles, $\dot{\Theta}$ is the vector of joint velocities, and the diagonal matrices Q_{Θ} and $Q_{\dot{\Theta}}$ represent weighting of costs for deviation from final desired posture, marked by subscript 'f'. Let T_{work} represent the shoulder and elbow torques that minimize the cost function in Eq. (1). We propose that movements are initiated using these torques, and towards the end of movement, impedance mechanisms take over. We represent this mathematically as,

$$T = (1-w) \underbrace{T_{work}}_{predictive} + w \underbrace{\left(-K (\Theta - \Theta_f) - B (\dot{\Theta} - \dot{\Theta}_f) \right)}_{impedance} \quad (2)$$

where K and B are diagonal matrices representing stiffness and viscosities across shoulder and elbow. w is a switching function that describes when the switch between predictive and impedance mechanisms occurs. At the start of the movement, $w = 0$ represents a purely predictive scheme, and at the end of the movement, $w = 1$ represents a purely impedance scheme. The time of switch between the two modes is characterized by a parameter 's' such that,

$$w = \frac{1}{1 + \exp(-160(t - st_f))} \quad (3)$$

We call the parameter 's', the *switch instant*. If $s = 1$, the control law is purely predictive and if $s = 0$, the control is purely impedance. Our model described by Eqs. 1–3 is characterized by 9 parameters; the first 4 parameters represent the cost on trajectory errors and describe the predictive trajectory, the next is the switch instant and the final 4 represent stiffness and damping/viscosities at the elbow and shoulder joints. We computed these 9 parameters in 2 steps to minimize the error between the time course of movement and the figural distance between our simulated trajectory, and our experimental data. The first step approximated the predictive control strategy. The predictive mechanisms are fit to the initial part of the trajectory. This is achieved by having a greater cost for errors up to peak acceleration, and a lower cost for the overall trajectory. In the next step we computed the switch instant, as well as the stiffnesses and viscosities for the impedance controller. We used particle swarm

optimization to compute all controller parameters that best described the observed experimental data. The implementation of this method to compute controller parameters is described in greater detail in Yadav and Sainburg, 2011. The appendix outlines *pseudo-code* with the error functions and implementation scheme for both computational steps.

Simulations for model validation

To test the validity of a controller based on Eq 1–3, we chose values of the Qs [1000 1000 500 500], K and B [55 80 5 5] and held them constant while varying the switch instant from 0 to 1. We further performed a sensitivity analysis to quantify the effect of parameter variations on trajectory error. As our trajectory fit is nonlinear with respect to the parameters, it was possible that all the parameters need not influence the trajectory equally. We performed a Monte Carlo simulation where we sampled the parameters for either impedance or predictive mechanisms while holding the switch instant constant. Four thousand sets of controller parameters for predictive or impedance mechanisms were sampled from a normal distribution whose standard deviation was 10% of the mean value, and the resulting trajectory errors were computed for switch times ranging from 0.1 to 0.9. We varied all parameters for a particular mechanism to compute trajectory deviations. For the predictive mechanism, these were 4 parameters quantifying contributions of trajectory errors, and for the impedance mechanism, these were 4 parameters quantifying stiffnesses and viscosities at the shoulder and elbow joints. For the switch instant, the same simulations were performed by sampling switch time from a distribution with a standard deviation of 0.1 and mean values ranging from 0.1 to 0.9.

Metrics

We first confirmed that our model was able to approximate the observed experimental data accurately. To do so, we quantified the goodness of fit using 2 measures; coefficient of determination (R^2), and figural distance between two trajectories (Schabowsky et al., 2007). To compare the contributions of predictive and impedance mechanisms, we quantified the difference in the instant of switch for the nondominant and the dominant arm. We computed the instant of switch relative to the time of both peak acceleration and peak velocity, as well as the distance traveled by the time of the switch instant. These metrics are described in detail in Yadav and Sainburg, 2011. We also compared model parameters that describe predictive and impedance mechanisms between the two arms.

Statistical analysis

As we were mainly interested in interlimb differences in motor performance for each arm. We then compared differences between the dominant and nondominant arms using one-way ANOVA with arm as the within subject factor. Post-hoc comparisons were performed using pairwise t-tests with Bonferroni corrections when warranted by a statistically significant difference ($P < 0.05$).

Results

Model validation

To test the validity of the controllers based on Eq 1–3, we chose values of Qs [1000 1000 500 500], K and B [55 80 5 5] and held them constant while varying switch instant 's' from 0 to 1, the resulting hand paths are shown in Figure 2.

Note that the hand paths for lower values of 's' deviate laterally and are projected away from the straight line path to the target. For higher values of 's', the hand paths are straighter and show slight medial deviations. These results are in accordance with our previous findings for nondominant and dominant arm reaching trajectories, respectively (Sainburg and Kalakanis, 2000). Therefore, our computational model described by Eqs 1–3 has the potential to describe the trajectories of the dominant and nondominant arms.

Sensitivity analysis

We used a hybrid control scheme to approximate the movement trajectories of the subjects. However, due to the nonlinear relationship between the controller parameters and the resulting trajectory, the same variation in all parameters need not have had the same effect on the trajectories. To quantify the effect of individual parameter variations on the trajectory, we performed a Monte Carlo simulation where we varied the parameters for impedance control, predictive control, or switch time, while holding all other parameters constant. *We varied the parameters for the predictive controller as follows: Qs about mean values of [1000 1000 500 500], stiffnesses and viscosities for elbow and shoulder, Ks and Bs about mean values of [55 80 5 5]. The standard deviation of the distribution was 10% of the mean value. For switch time, we varied the mean value in the range of 0.1 to 0.9, with a standard deviation of 0.1. As we used switch time to characterize the control schemes, we performed simulations across the entire range of switch time to obtain finer resolution.*

Figure 3 presents the resulting trajectory errors for different variations. These results indicate that the hand paths were most-sensitive to changes in switch time and impedance parameters for the early switch times. Trajectory variations were less sensitive to changes in parameters for predictive control. This may be because the switch time and impedance parameters directly influenced the torque profiles, whereas the parameters for predictive mechanisms influenced the weighting of trajectory errors in the associated cost function. It should be emphasized that the trajectory variations were fairly insensitive to small variations in gains, yet the trajectory was defined by the optimization until the time of switch to the impedance controller. Thus, this sensitivity analysis indicated the degree to which variations in our parameters produced variations in the trajectory, not the degree to which each controller produced differing trajectories. In fact, the high sensitivity of the trajectory to our switch time parameter emphasizes the importance of each controller in contributing to the trajectory. In summary, our simulation was substantially sensitive to small variations in switch time, allowing us to use this parameter to characterize the relative contributions of the two control mechanisms.

Design Confirmation

Before comparing parameters from our data fitting to draw inferences about underlying control mechanisms of the dominant and nondominant arms, we first report how well our control model approximated the experimental data. Figure 4a) presents representative hand paths from our model and the experimental data. Our results indicate a good fit between experimental data and the trajectories from our fitted model. We next report R^2 (b) and figural distance (c) between the two trajectories. Overall, the dominant arm trajectories were better approximated by our model as indicated by both R^2 ($F(1,11)=11.26$, $p=0.0073^*$) and figural distance ($F(1,11)=10.69$, $p=0.0084^*$). This is not surprising given our model assumptions that the impedance mechanisms are characterized by fixed gains on joint angle and velocity errors. Humans generate limb stiffnesses and viscosities that are nonlinear and both position and velocity dependent (Gomi and Osu, 1998; Osu and Gomi, 1999). It is plausible that our simplification may have introduced errors. Nevertheless, our model did approximate the trajectories well, indicating that this model should be sufficient to provide information about the underlying control mechanisms. These results suggest that the dominant arm movements were predominantly controlled using predictive mechanisms. We next present metrics that quantify when the switch from predictive to impedance mechanisms occurred.

Contribution of predictive control

Switch instant—We quantified switch from predictive to impedance mechanisms using two metrics; 1) The instant at which the control scheme switched from predictive to impedance mechanisms and 2) the fraction of total distance traveled by the instant of switch. Figure 5a shows the mean $\pm$ standard errors for these two metrics. Our results indicate that the nondominant arm movements had lower switching instants, (i.e. the nondominant control scheme switched to the impedance mechanisms earlier than that of the dominant arm). One way ANOVA revealed a significant effect of arm ($F(1,11)=30.17$, $p=0.0003^*$) for switch instant. We next measured the fraction of total distance traveled by the instant of switch, Figure 5b). One-way ANOVA revealed a main effect of arm ($F(1,11)=28.49$, $p=0.0003^*$), such that the dominant arm traversed significantly larger distance using the predictive mechanisms.

Switch instant relative to peak acceleration and peak velocity—We next quantified the instant of switch between the predictive and the impedance mechanisms, relative to two key kinematic events, the time of peak acceleration and the time of peak velocity. Figure 6 presents mean $\pm$ SE plots for switch instant relative to instant of a) peak acceleration and b) peak velocity. Our results indicated that both the dominant and nondominant arms switched to impedance mechanisms after peak acceleration. However, the nondominant arm switched earlier than the dominant arm ($F(1,11)=43.27$, $p<0.0001^*$). For the nondominant arm, the switch to impedance mechanisms occurred near the time of peak velocity. However, this switch occurred much later in the movement for the dominant arm ($F(1,11)=27.11$, $p=0.0004^*$).

Overall, these findings indicate that the movements of the dominant and nondominant arms can be described by the same hybrid control scheme, in which movements are initiated using

predictive mechanisms, and terminated using impedance mechanisms. The nondominant arm movements were characterized by an earlier switch to impedance mechanisms, while the dominant arm movements showed greater contributions of predictive mechanisms. In the framework of this model, the control of dominant and nondominant arms are described by a hybrid control scheme that combines predictive and impedance mechanisms.

Controller parameters

We next investigated controller parameters that describe the predictive and impedance mechanisms.

Predictive control—Figure 7 presents measures that characterize our predictive control parameters. Figure 7a presents mean $\pm$ SE for the weighing of joint angular error relative to the desired final posture. Our results indicate no main effect of hand ($F(1,20) = 0.0604$, $p = 0.8083$), joint ($F(1,20) = 1.1080$, $P = 0.3051$) or hand by joint interaction ($F(1,20)=0.4928$, $p = 0.4908$) in the parameters that describe predictive mechanisms. In addition, no main effects of ($F(1,20) = 2.1296$, $p = 0.1600$), joint ($F(1,20) = 0.1544$, $P = 0.6985$) or hand by joint interaction ($F(1,20)=0.0022$, $p = 0.9630$) were observed for the weighing of joint velocity errors. Overall, there were no differences in the controller parameters that described predictive control.

Although these results suggest that the dominant and nondominant arm movements utilized similar predictive mechanisms, the trajectory errors were not sensitive to variations in predictive parameters. Therefore, it is not possible to determine whether the two arms might have used the same predictive mechanisms.

Impedance mechanisms—We next compared the controller parameters that described the impedance control mechanisms (Figure 8). Stiffness, the gain on positional error showed no main effect of hand ($F(1,20)=0.1461$, $P = 0.7063$), joint ($F(1,20)=1.3531$, $P = 0.2584$) or hand by joint interaction ($F(1,20)=3.0993$, $P = 0.0936$). However, viscosity, the gain on velocity error, showed a main effect of hand ($F(1,20)=17.5949$, $P = 0.0004^*$), but no main effect of joint ($F(1,20)=3.8760$, $P = 0.0630$) or hand by joint interaction ($F(1,20)=3.7437$, $P = 0.0673$). The dominant arm's movements were characterized by lower gains on velocity errors. Post-hoc comparisons revealed that the viscosity gain on velocity errors was lower for the dominant arm. This main effect of arm is likely due to the fact that the impedance controller was used to decelerate the non-dominant arm from peak velocity, whereas it was only used to stop the dominant arm at the end of the deceleration phase of motion.

Discussion

This study was done in order to examine plausible control mechanisms that might underlie lateralization within the motor system. Previous research has quantified preference and performance differences between the two arms (Carson 1990, Carson et al. 1993, Coelho et al, 2013; Roy and Elliot 1986,1989; Sainburg, 2005). Based on previous empirical studies, we have developed a bihemispheric model of motor lateralization (Sainburg, 2002) that proposes dominant hemisphere specialization for predicting arm and task dynamics, and non-dominant hemisphere specialization for controlling limb impedance. In order to

examine the plausibility of this control hypothesis, we developed a model of control that combines these two processes in series: Movements are initiated by the predictive controller, and ultimately movement termination is handled by a controller that specifies velocity and position dependent impedance about a final equilibrium posture. We chose a hybrid model and not a model where movements of each arm were explained solely by its own controller, i.e impedance mechanisms for the nondominant arm, and predictive mechanisms for the dominant arm. A pure impedance mechanism has been shown to be inadequate for movement production, mainly because of the requirement for non-biological control inputs at initiation, and non-biological stiffnesses required to generate those movements (Popescu et al, 2000; 2003a, 2003b). Further, human arm movements exhibit task-dynamic-dependent stiffness suggesting they involve some type of predictive controller (Gomi and Osu, 1998). However, if movements are initiated using a predictive strategy, these issues can be resolved. Having a purely predictive scheme results in trajectories that are more sensitive to perturbations or unexpected changes in movement or task dynamics (Ghez et al. 2004, 2007). In addition, sensory uncertainty that arises during the movement would make stopping near impossible, and the limb would become unstable at the intended movement termination. Thus, a pure impedance control scheme is robust but not optimal, and a pure predictive control scheme is optimal but not robust. A hybrid control solution overcomes the limitations inherent in each individual control mechanism.

Similar serial hybrid models have been used to study mechanisms involved in motor adaptation to identify separate mechanisms for control of trajectory and position (Schiedt and Ghez, 2007). We fit our simulations to dominant and nondominant trajectories obtained from experiments, by allowing modification of 9 variables: two control gains in our predictive controller, and two impedance constants in our impedance controller at shoulder and elbow joints. The fifth parameter was the time that control switched between the two modes. For each recorded movement, using the geometric and inertial characteristics fit to each subject, we computed parameters of our model to best approximate an average trajectory to each target. In our model of control, the control scheme is the same between the two arms, however, the parameters that characterize these controllers are different. We could have fit our model so that the parameters for predictive and impedance controllers were the same between the arms. However, this would have assumed, apriori, that both the arms use both controllers in a similar manner. We followed a more rigorous approach in this study, where independent fits were done to the trajectories of the two arms. As indicated by our results, the two schemes employed impedance control differently. The nondominant arm appeared to exploit impedance mechanisms to drive the movement, while the dominant arm employed impedance mechanisms late in the deceleration phase to stop the motion.

Our model fit the movements of both arms well, as indicated by our R^2 and figural deviation measures. However, the fit for dominant arm movements was slightly better than that for nondominant arm movements. This might be related to the rather simple nature of our impedance model. While we could not confirm if predictive mechanisms were different, the impedance constants were different for the two arms. We speculate that this was related to the fact that the impedance controller was responsible for accelerating motion of the nondominant arm, while it simply acted at the very end of movement deceleration for the

dominant arm. Finally, and most important, the time of switch varied systematically for the two arms. Dominant arm movements were characterized by a late switch, near the end of motion to the impedance control scheme, while the nondominant arm movements were characterized by a switch that occurred early in movement. These results corroborate our findings showing the same pattern of switch instances for a prior control simulation governing single joint movements (Yadav and Sainburg, 2011).

We previously presented a similar computational model based on a serial hybrid control scheme, in which movements of *each* arm were initiated with a predictive, optimal control strategy and terminated with a final position controller that uses “impedance” mechanisms, to stabilize the arm at a goal position. When this model was fit to experimentally observed dominant, right and non-dominant, left arm movements of healthy young right-handers (Sainburg and Schaefer, 2004), left arm movements were characterized by an early switch from the predictive to the position control policy, while dominant arm movements were characterized by a late switch. Thus, while movements of both arms were initiated and terminated using the predictive and impedance strategies respectively, the critical difference between the two arms was characterized by *when* the switch from predictive to positional control occurred. However, that study only characterized the time course of the trajectory of single joint movements. Our findings in this study extend those of our previous study by indicating that the systematic differences in trajectory curvature between the arms during multijoint reaching movements can be accounted for by a serial hybrid model of control, based on our model of motor lateralization. The different curvatures of the nondominant and dominant arms could be accounted for by the time of switch between the two controllers. When the switch occurred early in non-dominant arm motion, curvatures were directed laterally early in movement due to the influence of intersegmental interaction torques (Sainburg and Kalakanis, 2000). However, when predictive control continued to direct the trajectory throughout most of the movement, curvatures were lower and initially directed medially, a strategy that reduces the displacement of the center of mass of the arm from the shoulder (Bagesteiro and Sainburg, 2002), thereby reducing inertial resistance to acceleration.

Our serial hybrid control model draws on modes of control that are thought to be differentially mediated by each hemisphere. This is consistent with previous studies indicating that motor cortical areas of both brain hemispheres are active during unilateral movements, including tapping (Cramer et al., 1999), sequencing (Kim et al., 1993; Kawashima et al., 1993, 1998), arm reaching (Nirkko et al. 2001), and planning and pantomiming (Frey et al., 2005) of tool actions. However, the most substantial support for this type of bihemispheric control comes from studies of stroke survivors with damage to either the left or right hemisphere. Such patients show significant deficits in coordination and timing of the ipsilesional arm, despite the fact that the contralesional hemisphere is not damaged (Winstein and Pohl, 1995; Haaland, 2007; Haaland et al., 2004; Desrosiers et al., 1996). More importantly, these deficits are different, depending on whether the left or right hemisphere has been damaged (Winstein and Pohl, 1995; Schaefer et al. 2007, 2009a; Mutha et al; 2011a, 2011b). In fact, hemisphere dependent deficits have been shown to be expressed in both the ipsilesional and contralesional arms (Mani et al. 2013; Mutha et al;

2011a, 2011b). For example, left hemisphere damaged patients show deficits in adapting initial movement direction and handpath curvature to novel visuomotor perturbations when moving with their contralesional (Mutha et al., 2011b) as well as their ipsilesional arms (Mutha et al., 2011a;). In contrast, right hemisphere damage results in poor movement accuracy, but spares trajectory control and adaptation deficits (Mutha et al. 2011a; Schaefer et al., 2009a, 2009b). Thus, while both hemispheres appear to cooperate for control of each arm in healthy subjects, damage to only one hemisphere will produce specific deficits in both arms. Understanding the nature of these deficits is critical for clinical rehabilitation professionals, who must optimize functioning after subjects have suffered a unilateral stroke. While it has been recognized for many decades that the non-paretic arm suffers coordination and control deficits (Wyke, 1981; Haaland, 2007; Deroseir, 1996), it has recently been shown that such deficits can produce substantial deterioration in performance in activities of daily living (Derosier 1996; Scheafer, 2009a). This is not difficult to understand, given the enhanced role of the nonparetic arm in functioning. In fact, this arm must become the major manipulator for an individual, whether it was the dominant or nondominant arm prior to the stroke. We have previously directly linked the functional deficits in performance of activities of daily living to the hemisphere specific deficits that result from ipsilateral left or right hemisphere damage (Schaefer, 2009a). Our current results clarify the nature of the control processes that might be specialized to each hemisphere, and can provide insight for the design of hemisphere specific physical rehabilitation that might target impedance or predictive mechanisms, depending on the side of the lesion.

Earlier studies have characterized handedness as a specialization of the dominant system for skilled performance. However, this study provides support to the idea that control of both arms has become specialized for different aspects of motor control. The asymmetry associated with handedness reflects unequal contributions of each process to one or the other arm. The arm contralateral to a hemisphere reflects a more dominant influence of that hemisphere's control mechanisms. This hybrid scheme can account for not only asymmetries in trajectory control that advantage the dominant arm for trajectory smoothness, efficiency, and adaptation, but also for asymmetries in impedance control that advantage the nondominant arm for positional accuracy (Przybyla et al., 2013), as well as for responses to unpredictable dynamic events (Bagesteiro and Sainburg, 2003; Yadav and Sainburg, 2014). Indeed this type of control should lead to advantages of each arm under different conditions. The dominant arm should be advantaged when environmental conditions are predictable, while the nondominant arm should be advantaged under unpredictable environmental conditions.

We recently tested this prediction by an experiment with two different force field environments, a field with a predictable magnitude that varies with the square of velocity, and a field with a less predictable magnitude that varies linearly with velocity. These fields were designed to be compatible with controllers that are specialized in predicting limb and task dynamics, and modulating position and velocity dependent impedance, respectively. Because the velocity square field did not change the form of the equations of motion for the reaching arm, we reasoned that a forward dynamic-type controller should perform well in this field, while control of linear damping and stiffness terms should be less effective. In contrast, the unpredictable linear field should be most compatible with impedance control,

but incompatible with predictive dynamics control. Our results confirmed that each arm made straighter, smoother, and quicker movements in its compatible field. In addition, each arm showed limited adaptation to its incompatible field. Analysis of the dependence of trajectory errors on field magnitude suggested that dominant arm adaptation occurred by prediction of the mean field, thus exploiting predictive mechanisms for adaptation to the unpredictable field.

In summary, our current results confirm the plausibility of our control based hypothesis of a bihemispheric, hybrid control of each arm, in which the dominant hemisphere provides predictive control of arm and task dynamics, while the non-dominant hemisphere is specialized for impedance control. While this model is consistent with previous empirical research, the current findings support the control-based mechanisms associated with this hypothesis.

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References

- Aboitiz F, López J, Montiel J. Long distance communication in the human brain: timing constraints for interhemispheric synchrony and the origin of brain lateralization. *Biol Res.* 2002; 36:89–99. [PubMed: 12795208]
- Annett J, Annett M, Hudson PTW. The control of movement in the preferred and non-preferred hands. *Q J Exp Psych.* 1979; 31:641–652.
- Bagesteiro LB, Sainburg RL. Handedness: dominant arm advantages in control of limb dynamics. *J Neurophysiol.* 2002; 88(5):2408–21. [PubMed: 12424282]
- Bagesteiro LB, Sainburg RL. Nondominant arm advantages in load compensation during rapid elbow joint movements. *J Neurophysiol.* 2003; 90(3):1503–13. [PubMed: 12736237]
- Bogen, JB.; Sperry, RW.; Vogel, PJ. Commissural section and the propagation of seizures. In: Jasper, Ward; Pope, editors. *Basic Mechanisms of the Epilepsies*. Boston: Little, Brown; 1969. p. 439
- Carson RG. Manual asymmetries: Old problems and new directions. *Human Movement Science.* 1993; 12(5):479–506.
- Carson RG, Chua R, Elliott D, Goodman D. The contribution of vision to asymmetries in manual aiming. *Neuropsychologia.* 1990; 28(11):1215–1220. [PubMed: 2290495]
- Cramer SC, Finklestein SP, Schaechter JD, Bush G, Rosen BR. Activation of distinct motor cortex regions during ipsilateral and contralateral finger movements. *J Neurophysiol.* 1999; 81:383–7. [PubMed: 9914297]
- Coelho CJ, Przybyla A, Yadav V, Sainburg RL. Hemispheric differences in the control of limb dynamics: a link between arm performance asymmetries and arm selection patterns. *J Neurophysiol.* 2013 Feb; 109(3):825–38. [PubMed: 23155169]
- Desrosiers J, Bourbonnais D, Bravo G, Roy PM, Guay M. Performance of the “unaffected” upper extremity of elderly stroke patients. *Stroke.* 1996; 27:1564–70. [PubMed: 8784131]
- Duff SV, Sainburg RL. Lateralization of motor adaptation reveals independence in control of trajectory and steady-state position. *Exp Brain Res.* 2007; 179(4):551–61. [PubMed: 17171336]
- Elliott D, Roy EA, Goodman D, Carson RG, Chua R, et al. Asymmetries in the preparation and control of manual aiming movements. *Can J Exp Psychol.* 1993; 47(3):570–589.
- Frey SH, Funnell MG, Gazzaniga MS. A Dissociation between the Representation of Tool-use Skills and Hand Dominance: Insights from Left- and Right-handed Callosotomy Patients. *J Cog Neurosci.* 2005; 17(2):262–272.

- Gazzaniga MS. Cerebral specialization and interhemispheric communication: does the corpus callosum enable the human condition? *Brain*. 2000; 123:1293–326. [PubMed: 10869045]
- Gazzaniga MS. The split brain revisited. *Scientific American*. 1998; 279(1):50–55. [PubMed: 9648298]
- Ghez C, Dinstein I, Cappell J, Scheidt RA. Posture and movement are encoded in different coordinate systems. *Soc Neurosci Abstr*. 2004; 873:14.
- Ghez C, Scheidt RA, Heijink H. Different learned coordinate frames for planning trajectories and final positions in reaching. *J Neurophysiol*. 2007;3614–3626. [PubMed: 17804576]
- Gomi H, Osu R. Task-dependent viscoelasticity of human multijoint arm and its spatial characteristics for interaction with environments. *J Neurosci*. 1998; 18(21):8965–8978. [PubMed: 9787002]
- Haaland KY. Hemispheric Dominance for Different Aspects of Movement. *Motor Control*. 2007; 11(Supplement):S7–S8.
- Haaland KY, Elsinger CL, Mayer AR, Durgerian S, Rao SM. Motor sequence complexity and performing hand produce differential patterns of hemispheric lateralization. *J Cogn Neurosci*. 2004; 16(4):621–636. [PubMed: 15165352]
- Herculano-Houzel S. Coordinated scaling of cortical and cerebellar number of neurons. *Front Neuroanat*. 2010; 4:12. [PubMed: 20300467]
- Kim SG, Ashe J, Hendrich K, Ellermann JM, Merkle H, Ugurbil K, Georgopoulos AP. Functional magnetic resonance imaging of motor cortex: hemispheric asymmetry and handedness. *Science*. 1993; 261:615–617. [PubMed: 8342027]
- Kawashima R, Yamada K, Kinomura S, Yamaguchi T, Matsui H, Yoshioka S, Fukuda H. Regional cerebral blood flow changes of cortical motor areas and prefrontal areas in humans related to ipsilateral and contralateral hand movement. *Brain Res*. 1993; 623:33–40. [PubMed: 8221091]
- Kawashima R, Matsumura M, Sadato N, Naito E, Waki A, Nakamura S, Matsunami K, Fukuda H, Yonekura Y. Regional cerebral blood flow changes in human brain related to ipsilateral and contralateral complex hand movements—a PET study. *Eur J Neurosci*. 1998; 10:2254–2260. [PubMed: 9749754]
- Mani S, Przybyla A, Good D, Haaland K, Sainburg RL. Contralesional motor deficits after unilateral stroke reflect hemisphere-specific control mechanisms. *Brain*. 2013; 136(4):1288–303. [PubMed: 23358602]
- Mutha PK, Sainburg RL, Haaland KY. Critical neural substrates for correcting unexpected trajectory errors and learning from them. *Brain*. 2011a; (12):3647–3661. [PubMed: 22075071]
- Mutha PK, Sainburg RL, Haaland KY. Left parietal regions are critical for adaptive visuomotor control. *J Neurosci*. 2011b; 31(19):6972–81. [PubMed: 21562259]
- Nirkko AC, Ozdoba C, Redmond SM, Burki M, Schroth G, Hess CW, Wiesendanger. Different ipsilateral representations for distal and proximal movements in the sensorimotor cortex: activation and deactivation patterns. *Neuroimage*. 2001; 13:825–35. [PubMed: 11304079]
- Oldfield RC. The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia*. 1971; 9:97–113. [PubMed: 5146491]
- Osu R, Gomi H. Multijoint Muscle Regulation Mechanisms Examined by Measured Human Arm Stiffness and EMG Signals. *J Neurophysiol*. 1999; 81(4):1458–1468. [PubMed: 10200182]
- Popescu FC, Rymer WZ. End points of planar reaching movements are disrupted by small force pulses: an evaluation of the hypothesis of equifinality. *J Neurophysiol*. 2000; 84:2670–2679. [PubMed: 11068008]
- Popescu FC, Rymer WZ. Implications of low mechanical impedance in upper limb reaching movements. *Motor Control*. 2003a; 7:323–327. [PubMed: 14999131]
- Popescu FC, Hidler JM, Rymer WZ. Elbow impedance during goal-directed movements. *Exp Brain Res*. 2003g; 152:17–28. [PubMed: 12879184]
- Przybyla A, Coelho CJ, Akpınar S, Kirazci S, Sainburg RL. Sensorimotor performance asymmetries predict hand selection. *Neuroscience*. 2013; 228:349–60. [PubMed: 23111126]
- Rilling JK, Insel TR. Differential expansion of neural projection systems in primate brain evolution. *NeuroReport*. 1999; 10:1453–1459. [PubMed: 10380962]

- Rogers LJ. The two hemispheres of the avian brain: their differing roles in perceptual processing and the expression of behaviour. *J Ornithology*. 2012; 153(1):61–74.
- Rogers, LJ.; Vallortigara, G.; Andrew, RJ. *Divided Brains: The Biology and Behaviour of Brain Asymmetries*. Cambridge University Press; 2013.
- Roy EA, Elliott D. Manual asymmetries in visually directed aiming. *Can J Psychol*. 1986; 40(2):109–121. [PubMed: 3730950]
- Roy EA, Elliott D. Manual asymmetries in aimed movements. *Qtr J Exp Psychol*. 1989; 41(3):501–516.
- Sainburg RL. Evidence for a dynamic-dominance hypothesis of handedness. *Exp Brain Res*. 2002; 142(2):241–58. [PubMed: 11807578]
- Sainburg RL. Handedness: differential specializations for control of trajectory and position. *Exercise and Sport Sciences Reviews*. 2005; 33(4):206–213. [PubMed: 16239839]
- Sainburg, RL. Lateralization of Goal Directed Movements in Vision and Movement. In: Elliott, Digby; Kahn, Michael, editors. *Control of Goal-Directed Action*. Human Kinetics; 2010.
- Sainburg RL, Kalakanis D. Differences in control of limb dynamics during dominant and nondominant arm reaching. *J Neurophysiol*. 2000; 83(5):2661–2675. [PubMed: 10805666]
- Sainburg RL, Schaefer SY. Interlimb differences in control of movement extent. *J Neurophysiol*. 2004; 92(3):1374–83. [PubMed: 15115793]
- Sainburg RL, Wang J. Interlimb transfer of visuomotor rotations: independence of direction and final position information. *Exp Brain Res*. 2002; 145(4):437–447. [PubMed: 12172655]
- Schabowsky CN, Hidler JM, Lum PS. Greater reliance on impedance control in the non-dominant arm compared with the dominant arm when adapting to a novel dynamic environment. *Exp Brain Res*. 2007; 182(4):0567–577.
- Shadmehr R, Mussa-Ivaldi FA. Adaptive representation of dynamics during learning of a motor task. *J Neurosci*. 1994; 14:3208–3224. [PubMed: 8182467]
- Schaefer SY, Haaland KY, Sainburg RL. Ipsilesional motor deficits following stroke reflect hemispheric specializations for movement control. *Brain*. 2007; 130(Pt 8):2146–58. [PubMed: 17626039]
- Schaefer SY, Haaland KY, Sainburg RL. Hemispheric specialization and functional impact of ipsilesional deficits in movement coordination and accuracy. *Neuropsychologia*. 2009a; 47(13):2953–66. [PubMed: 19573544]
- Schaefer SY, Haaland KY, Sainburg RL. Dissociation of initial trajectory and final position errors during visuomotor adaptation following unilateral stroke. *Brain Res*. 2009b; 1298:78–91. [PubMed: 19728993]
- Scheidt RA, Ghez C. Separate adaptive mechanisms for controlling trajectory and final position in reaching. *J Neurophysiol*. 2007; 98:3600–3613. [PubMed: 17913996]
- Sperry RW. Cerebral organization and behavior. *Science*. 1961; 133:1749–1757. [PubMed: 17829720]
- Wang J, Sainburg RL. The dominant and nondominant arms are specialized for stabilizing different features of task performance. *Exp Brain Res*. 2007; 178(4):565–70. [PubMed: 17380323]
- Winstein CJ, Pohl PS. Effects of unilateral brain damage on the control of goal-directed hand movements. *Exp Brain Res*. 1995; 105(1):163–174. [PubMed: 7589312]
- Wyke MA. The nature of cerebral specialization in man: Quantitative vs qualitative differences. *Behav and Brain Res*. 1981; 4(1):78–79.
- Yadav V, Sainburg RL. Motor lateralization is characterized by a serial hybrid control scheme. *Neuroscience*. 2011; 196:153–167. [PubMed: 21889579]
- Yadav V, Sainburg RL. Limb dominance results from Asymmetries in Predictive and Impedance Control Mechanisms. *PloS one*. 2014; 9(4):e93892. [PubMed: 24695543]

Appendix A

This Appendix presents the numerical algorithm used to fit the controller parameters to the experimental data. We fit our data in two steps, the first step is to compute parameters that describe the predictive scheme. The pseudocode for computation is described below,

Initialization

1. Set range of controller parameters to [1500 1500 1000 1000].
2. Set number of particles to 8000, and define initial values for each particle.

Optimization to compute controller parameters

1. For each set of parameters (P_i), compute optimal trajectory
2. Calculate initial trajectory error as sum of R-square and figural distance (fig_err) for each particle in the swarm. These are computed for errors until peak acceleration and entire trajectory. Take weighted sum of error until peak acceleration ($R_sq_{max\ a}$) and total trajectory (R_sq_{total}).

$$\min \{0.1R_sq_{total}+0.9R_sq_{max\ a}+0.1fig_err\} \quad (A.1)$$

3. Store the best solution ($P_{i,best}$) observed by each particle, and the best solution attained by the entire group (P_{global_best}).
4. Update next particle as average of current value, group best, individual best and random values to allow for exploration.

$$P_i=0.25 P_i+0.25 P_{i,best}+0.25 P_{global_best}+0.25 P_{random} \quad (A.2)$$

5. Repeat 1 to 4 8000 times.

The next step involves computation of

Initialization

- 3 Set range of parameters to [100 100 10 10 1].
- 4 Set number of particles to 8000, and randomized initial values for each particle.

Optimization to compute controller parameters

- 6 For each set of parameters (P_i), compute optimal trajectory
- 7 Calculate initial trajectory error as sum of R-square and figural distance for each particle in the swarm.

$$\min \{0.5 R_sq_{total}+0.5 fig_err\} \quad (A.3)$$

- 8 Store the best solution observed by each particle($P_{i,best}$), and the best solution attained by the entire group (P_{global_best}).
- 9 Update next particle as average of current value, group best, individual best and random values to allow for exploration.

$$P_i = 0.25 P_i + 0.25 P_{i,best} + 0.25 P_{global_best} + 0.25 P_{random} \quad (A.4)$$

- 10 Repeat 1 to 4 8000 times.

Research Highlights

1. Handedness explained using computational model.
2. Dominant/nondominant arm movements explained using the same hybrid controller
3. Predictive and impedance mechanisms for each arm are not different
4. Predictive and Impedance mechanisms weighed differently for each arm
5. Dominant arm relies on predictive and nondominant arm on impedance mechanisms

Figure 1.
Experimental apparatus.

Figure 2.
Hand paths for different values of switch instant ' s '. Values of ' s ' are displayed below the hand paths. Squares indicate the switch instants.

Figure 3. Trajectory errors due to variations in switch time, predictive or impedance parameters.

Figure 4.

a) Representative hand paths from our controller model and experimental data for the dominant and nondominant arms. Small squares indicate the switch from predictive to impedance controller. b) R-square and c) Figural distance for the dominant and nondominant arms.

Figure 5.

a) Switch instant between predictive and impedance control, and b) Fraction of distance traveled using predictive control for the dominant and nondominant arms.

Figure 6.

a) Switch instant with respect to peak velocity location, and b) Switch instant with respect to peak acceleration location for the dominant and nondominant arms.

Figure 7. Weighing on a) joint angle position error and b) velocity error for the dominant and nondominant arms.

Figure 8. Controller gains for a) joint angle position error (stiffness) and b) velocity error (viscosity) for the dominant and nondominant arms.