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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 rightdominant arm, while the duration of the initial acceleration profile scaled greater with movement speed for the leftnon-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 righthemisphere 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. © 2016 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: motor learning, interlimb transfer, generalization of learning, motor lateralization, neural lateralization, crosseducation

E-mail address: rls45@psu.edu (R. L. Sainburg). *Abbreviations*: LHD, left hemisphere damage; LQ, laterality quotient; RHD, right hemisphere damage.

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INTRODUCTION

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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 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, 2002; 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

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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, guantified 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 aftereffects, 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). Mafait 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, 2004; 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 (RHD) (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.

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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.

EXPERIMENTAL PROCEDURES

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 counterbalanced 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 these 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.

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