The Pennsylvania State University

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LATERALIZATION AND INTERLIMB TRANSFER IN DE NOVO LEARNING OF A 2-D REDUNDANT SHUFFLEBOARD GAME

A Thesis in

Kinesiology

by

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ABSTRACT

We extend a previously proposed hypothesis of motor lateralization that attributes predictive control of limb trajectories to the dominant hemisphere and control of limb position and posture to the non-dominant hemisphere. This hypothesis is supported by studies demonstrating sensorimotor adaptation during visuomotor rotations in patients with focal cortical lesions. However, it is not known whether specialization of the dominant system will also be reflected in the learning of a de novo task, a task that requires learning of a novel movement. We now ask whether lateralization of motor learning will occur during learning of a task that requires predictive control of hand trajectory. In our task, participants hit a virtual puck from a central location toward a 180° arc located 35 cm from the initial puck position. Participants were free to start each trial anywhere behind a horizontal line located 10 cm posterior to the puck. Hand velocity was transferred to the puck at impact depending on the location of impact and on the magnitude and direction of the hand velocity vector. Thus, accurate performance required coordinated control of hand velocity and impact location. Sixteen right-handed young adults performed the task with both arms for two consecutive days: Eight participants performed with their dominant arm first and then with their non-dominant arm, while eight participants performed in the reverse order. Both arms showed a rapid reduction of task error in the beginning, then maintained the error level throughout the session. There was no significant effect of handedness in learning of the task. Moreover, both arms showed not significantly different mean and variance in the movement initiation location after the participant learned the task. Both arms showed a reduction of task error during the subsequent task performance followed by the training with the initial arm. We propose that both hemisphere-limb systems developed similar models of control through learning. As a result, both arms showed a similar reduction in task error throughout the learning and the transfer of learning. We suggest that the effect of handedness is not prominently

demonstrating on a planar skilled task when redundant degrees of freedom are allowed during the movement.

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Chapter 1

Introduction

The enhanced performance of trained individuals brings huge amusement to crowds. In any professional sport, the athletes are evaluated by their performance during the game, and teams with highly skilled athletes who show remarkable performance are beloved by numerous fans. People practice and train their physical and mental skills for many years to compete at the professional level. In Olympics games, athletes break world records by demonstrating performance with faster, stronger, and more precise physical ability. Although we witness incredible improvement in performance as a result of training, the detailed mechanism responsible for such changes is yet to be completely understood.

In the field of movement science, motor learning has been widely studied through paradigms of adaptation learning, which entails relearning motor behavior in an unusual environment. There is another type of motor learning, called skill learning, which covers a different spectrum of motor learning: the improvement of performance beyond a baseline level. The improvement of performance accompanies the increase of movement accuracy and movement precision. To understand how skilled performance is developed and how movement errors are regulated, researchers have analyzed motor variability. While there are several methods for analyzing motor variability, the Goal Equivalent Manifold (GEM) analysis suggests a mathematical approach to understanding how the error regulation process occurs during task performance.

In the task performance of skilled activities such as playing sports or musical instruments, the dominant arm and the non-dominant arm play very different roles. However, few studies have investigated why such a division in roles exists or the mechanisms behind the specialized role of each arm in performing the skilled task. Understanding how the specialized role of each arm contributes to skill learning would offer practical implications for the rehabilitation of neurologically impaired patients and athletic training.

In this section of the thesis, I describe three research themes with a brief review of previous studies conducted along those themes. The themes are motor learning, which addresses a change in motor behavior or control due to practice; motor redundancy and variability; and the lateralization of motor control processes. In the end, I propose a novel experiment that addresses the research questions of these three research themes.

Motor learning – Adaptation and Skill

In sensorimotor learning literature, there are two types of motor learning: skill and adaptation (Krakauer, Hadjiosif, Xu, Wong, & Haith, 2019; Krakauer & Mazzoni, 2011; Sternad, 2018). Both types of motor learning drive change in motor behavior through practice and experience. Adaptation learning has been defined as motor learning that takes place when well-established movements, including walking, reaching, and postural control are re-learned in an unusual environment. Skill learning, on the other hand, occurs when executing more complex movements and activities, such as learning to play a new instrument or a new sport. Although it is hard to sharply distinguish between skill learning and adaptation learning, researchers have developed different experimental paradigms to investigate each.

Adaptation learning

Lackner and Dizio (1994) instructed participants to make a point-to-point rapid reaching movement to a specified target under a Coriolis force perturbation created in a rotating room. In the rotating room, the Coriolis force perturbs the arm of the participant in the opposite direction of rotation as they reach outward from the center of the room. Throughout the experiment, participants first performed a set of reaching tasks without the perturbation (pre-rotation). Then, they performed a second set of reaching tasks with the perturbation (per-rotation). In the last set, they again performed without the perturbation (post-rotation). In the pre-rotation phase, participants made a straight movement from the starting position to the target (Figure 1A). When the room started to rotate, participants initially showed a large deviation from the straight trajectory toward the target in the direction of the Coriolis force. Over the course of multiple trials, they soon reduced the extent of deviation, and they eventually learned to make a straight movement in the rotating room (Figure 1A). Interestingly, as soon as the perturbation was turned off in the post-rotation phase, participants showed an identical magnitude of deviation in the reaching trajectory and the endpoint, in a direction opposite from the direction of the previously exerted Coriolis force (Figure 1B).

Such an aftereffect has been thought to be the outcome of learned compensation in movement during the process of adapting to the perturbation. This aftereffect is a typical feature of adaptation learning, and it suggests that there were sensorimotor re-mappings in the central nervous system (CNS) that changed the way participants performed the task. Shadmehr & Mussa-Ivaldi (1994) explain the aftereffect as a result of an internal model, a mapping between the predicted movement and the observed movement, in the CNS. This feature has become a well-known phenomenon because it was consistently observed in other adaptation studies with various types of perturbations, such as visuomotor rotation (Wigmore, Tong, & Flanagan, 2002), extra loads (Sainburg, Ghez, & Kalakanis, 1999), viscous force fields (Shadmehr & Mussa-Ivaldi, 1994), and reflected vision through prism glasses (Morton & Bastian, 2004).

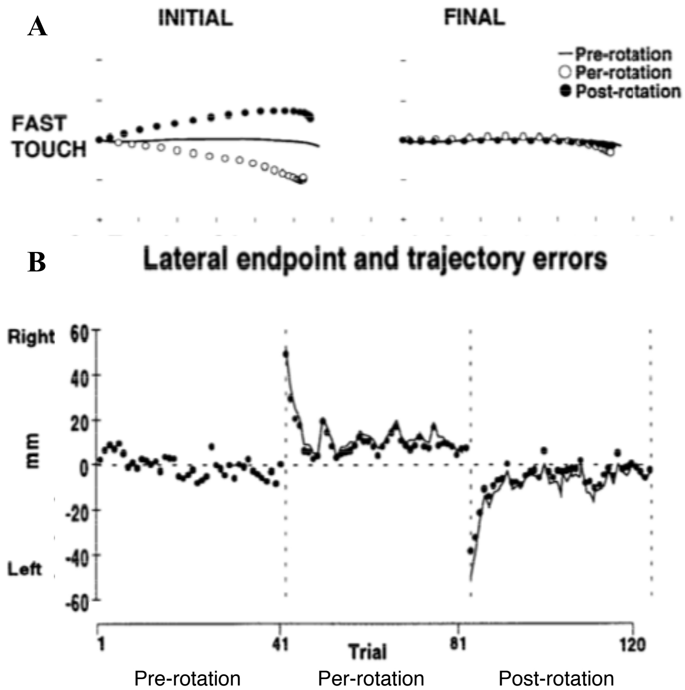


Figure 1 Results from the experiment of Lackner and Dizio. A: averaged hand trajectories in each set of reaching from the top view. B: plots of lateral endpoint and trajectory errors for all trials. Dots represent lateral endpoints positions and lines represent the peak lateral trajectory positions. This figure is directly adapted from the original report (Lackner & Dizio, 1994).

Researchers have further investigated adaptation learning to determine whether motor memory is retained after the initial learning. Braschers-Krug et al. (1996) investigated whether motor learning due to adaptation could be retrieved 24 hours after the initial practice. They instructed participants to practice a point-to-point reaching task with a robotically controlled handle that formed a viscous force field. Participants practiced the movement and learned to control their hand in the force field. Twenty-four hours after the initial practice, researchers instructed the participants to perform the same task with the same force field. Participants showed significantly better performance when re-exposed to the same force field than they did initially, suggesting that the motor learning formed through the adaptation process from previous training is retained for at least 24 hours. In a subsequent study, Nezafat et al. (2001) demonstrated that the retention of learning in the same adaptation could occur up to 29 days after the initial learning. These studies on adaptation learning show how people correct goal-directed movement when they experience sensory prediction errors from an artificially created environment and how they retain the motor learning established through the correction. Subsequent researchers have followed up on this work to investigate neurophysiology in humans, particularly related to brain areas responsible for movement corrections in novel environments. In the past decades, significant insights on motor function deficits in neurologically injured patients have been established through this line of work.

Skill learning

In contrast to adaptation learning, experiments in skill learning address the aspect of motor learning related to training that enhances sensorimotor skills to a level beyond baseline performance. In general experiments on skill learning, participants learn to perform a new task that requires practice to increase the task performance in an unperturbed environment. In the experiment of Shumelof et al. (2012), researchers asked participants to practice an arc-pointing task for five consecutive days, and measured the change in their task performance. Participants were asked to follow a circular path by controlling a cursor shown on the screen with a wrist flexion-extension and pronation-supination movement (Figure 2). The goal of this task was to move a cursor from one target to another through the presented circular channel, in a clockwise direction. Researchers assigned participants into four groups, varying the movement time: medium (520–780 ms), slow (960–1440 ms), fast (360–540 ms), and control. Researchers measured the fraction of a trajectory within the channel, the movement time, and the mean and the variance of the trajectory on Day 1 through Day 5 to assess the change in skill level. On Days 2, 3, and 4, participants practiced the task within the assigned speed range, and they were tested on Days 1 and 5 in all speed ranges (slow, medium, and fast). The control group was exempt from the practice sessions on Days 2, 3, and 4 and tested only on Days 1 and 5. On average, participants in every speed range showed a significant increase in the in-channel fraction of the trajectory on Day 5. Representative trajectories from the fast group are shown at the top of Figure

2. In every group, participants reduced their movement time within the specified time ranges and reduced the variance of the trajectory (Figure 2, bottom). This suggests that the skill acquisition was associated not only with a large increase in accuracy, the in-channel fraction of trajectory, but also with a large increase in precision as shown in the trajectory variability reduction. The reduction of variability as a result of training has been shown in other skill-learning studies using a virtual skittles task (Cohen & Sternad, 2009; Muller & Sternad, 2004). The study by Shumelof et al. demonstrated a reduction in variability and error as participants learned the skill task, suggesting that there was an error-regulation process that contributed to improved accuracy and precision throughout the practice. However, how people regulate error in their hand trajectory was not examined.

While the mechanisms involved in motor learning have been mainly studied through adaptation learning, skill learning has been relatively less investigated. Due to different characteristics between adaptation and skill, more investigation of skill learning might offer a further understanding of the sensorimotor learning process in humans.

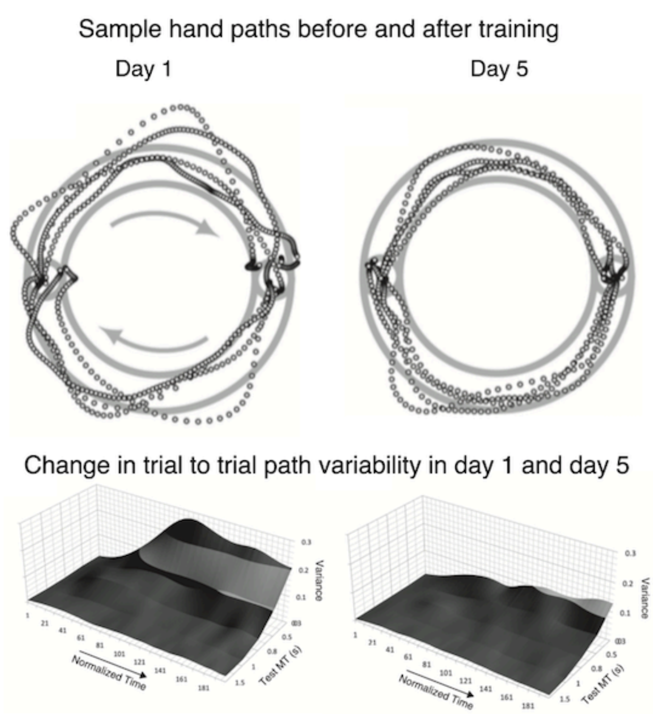


Figure 2 Results from the experiment of Shmuelof et al. Top: sample hand paths before and after training. Trajectories in a fast test speed condition were illustrated. After training (Day 5), more portions of the trajectory were drawn inside of the channel. Bottom: change in trial-to-trial path variability in Day 1 and Day 5. Less variance of the trajectory was shown in the task performance after training. This figure is directly adapted from the original report (Shmuelof, Krakauer, & Mazzoni, 2012).

Motor redundancy and variability

The human body has redundant degrees of freedom to perform any task (Bernshteĭn, 1967; Cusumano & Cesari, 2006; Latash, Scholz, & Schoner, 2002; Todorov & Jordan, 2002). How the CNS coordinates the redundancy that exists at multiple levels of the body system to produce a purposeful movement has been one of the major questions in the field of movement science (Cusumano & Cesari, 2006; Muller & Sternad, 2004; Todorov & Jordan, 2002). Due to this nature of the human body and the physiological noise involved in muscle activations, motor variability in human movement is an inevitable feature. Although this variability might provide information about the error-regulation process that allows us to perform tasks accurately, it has usually been regarded as noise and not analyzed in motor learning studies. Particularly in many studies of adaptation learning, researchers used paradigms with constrained movements in which most of the variability was already controlled by the task design. According to the Minimum Intervention Principle (MIP), Todorov& Jordan (2002) suggest that the variability originates from two main sources: one from the control effort and another one from the inherent noise in the movement. The MIP proposes that the CNS controls the variability that interferes with the movement toward goal achievement, but allows the variability that is not relevant to goal achievement. Researchers have suggested a number of different approaches to address the role of motor variability in motor control and learning (Cohen & Sternad, 2009; Cusumano & Cesari, 2006; John et al., 2016; Latash et al., 2002; Muller & Sternad, 2004; Todorov & Jordan, 2002).

One of these analyses is based on the Uncontrolled Manifold (UCM) hypothesis suggested by Latash et al. (2002). The UCM hypothesis assumes that, when the CNS wants to stabilize the level of task performance, it selects specific body elements within the available redundant elements that are directly relevant to the task performance. Latash and his colleagues demonstrate this by structuring the body elements in a task-specific subspace called “uncontrolled manifold" (UCM). This method hypothesizes that the CNS restricts the variability of the element that is not within the UCM, and it does not restrict the variability along the UCM. Latash et al. measure the ratio between the variance along the UCM and the variance orthogonal to the UCM, in order to demonstrate the extent of synergy between elements for a given task.

Another analysis is called the goal equivalent manifold analysis (GEM) (Cusumano & Cesari, 2006). In the GEM approach, the task-relevant variables are mathematically defined in the task design, and these variables form a solution space within the task space following the relationship with the goal. This solution space contains all combinations of task variables that lead to goal achievement in the task, so the solution space is termed the Goal Equivalent Manifold (GEM). In contrast to other analyses, there are no underlying assumptions about whether the CNS selects task-relevant variables, nor does the CNS restrict the variability of such task variables in the task space. The GEM analysis, therefore, is implemented in a task that has mathematically defined task variables necessary for goal achievement. In the paradigms for the GEM analysis, the goal function that mathematically explains the relationship between the task variables and the task goal is given. Also, the sensitivity that characterizes how the task variable variability gets mapped onto the GEM is defined. The GEM approach captures how the variability of the task variables relates to the goal-level task performance and how these are structured around the GEM.

In a study by John et al. (2016), GEM analysis was used to demonstrate how skilled human participants temporally and geometrically structure motor variability around the GEM during the performance of a skilled task. In this study, researchers devised a 1-D redundant virtual shuffleboard task with two task variables—the position (x) and the velocity (v) at the moment of release—that must be controlled to achieve a task goal. These task variables are defined precisely, rather than hypothetically, by the mathematical definition of the task. Here, the task was performed in a straight line that had a starting position and a target position, and the participants were asked to release the puck so that it stopped on top of the target position under the coefficient of friction. Once the task was performed, it yielded the task variables, a position (x) and a velocity (v) at the moment of release, and the task error (e). Task performance is solely determined by the task state (x, v) on a given trial. While there are infinite combinations of task variables—the task state (x, v)—that could lead to the goal, participants were allowed to choose any combination of task variables at their preference. The task state in every trial was mapped in the goal equivalent manifold (GEM). This plot formed the variability cloud around a mean operating point, which is the averaged task state ($\bar{x}, \bar{v}$), on the GEM. Then, the researchers

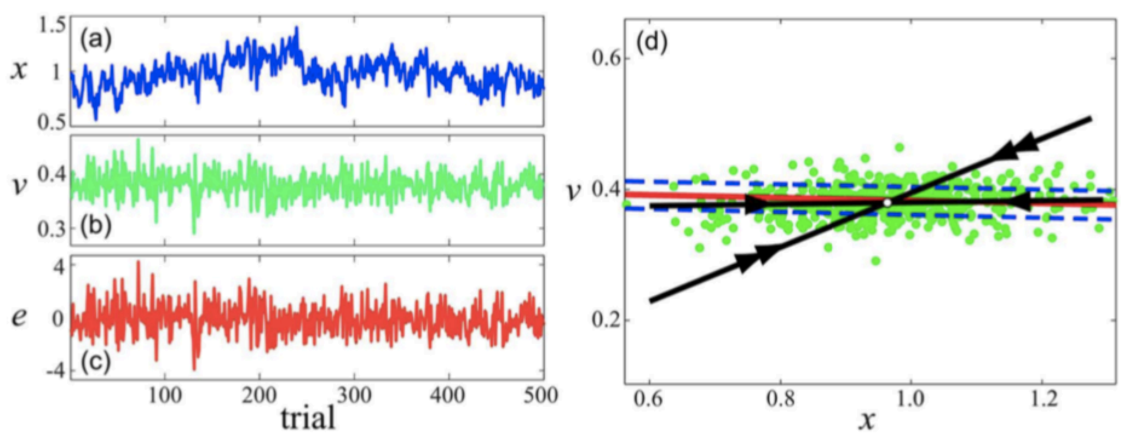


Figure 3 Results from the experiment of John et al. Representative data from a participant for a given friction condition. The trial-by-trial data of task error (e), release distance (x), and release velocity (v) are shown in graphs a-c. In graph d, the variability cloud structured by task variables from each trial is plotted. The white dot is the referenced mean operating point. The red line is GEM. The single arrow indicates the weakly stabled subspace and the double arrow indicates the strongly stabled subspace. The dashed blue line indicates ±10% goal-level contours. This figure is directly adapted from the original article (John, Dingwell, & Cusumano, 2016).

analyzed how the variability of task variables was structured in a trial-by-trial manner around the mean operating point with the time-series data of the task state (*x, v*) and task error (*e*), and the orientation of the variability cloud about the GEM (Figure 3). They found in all participants across the friction conditions that the mean operating points were within the 10% goal-level contour, which means that participants' task performance was close to zero task error. An inter-trial fluctuation structure analysis found that the system strongly regulates the direction of the task state when the task state for a given trial is placed transverse to the GEM. On the other hand, the system weakly regulates the direction of the task state when the task state for a given trial is placed along with the GEM. These results demonstrate that skilled participants quickly correct the variability transversely deviated from the GEM, but do not quickly correct the variability deviated along with the GEM, as they perform the 1-D shuffleboard task.

In this study, a detailed analysis of the variability structure reveals how the CNS coordinates the variables in the performance of a goal-directed task. This analysis also shows how the error-regulation process occurs in a trial-by-trial manner. While this study adopts a paradigm that limits movement of an end effector in one dimension, most of the tasks we perform daily involves with multiple dimensions. Given the ample biomechanical redundancy of the body system, an extended study on multiple dimensions will likely provide further understanding on how the system regulates the variability induced during the goal-directed movement with higher degrees of freedom.

Motor lateralization of control processes

When we perform any task, we tend to prefer using one hand over the other. This prominent feature of motor control called handedness, and it leads people to use each hand differently when performing a variety of tasks. For example, in baseball, right-handed catchers wear a glove on the left (non-dominant) hand and use the right (dominant) hand to throw the ball.

Similarly, when playing a musical instrument such as the cello, musicians hold a string note with their non-dominant hand and play with the dominant hand holding the bow.

In previous studies about handedness, researchers found that the dominant and non-dominant arms have a specific advantage for different aspects of a movement. Mutha et al. (2012) and Sainburg (2002, 2005) proposed a model of motor lateralization that attributes predictive control of limb trajectory to the brain's dominant hemisphere and control of limb impedance to the non-dominant hemisphere (Mutha, Haaland, & Sainburg, 2012; Sainburg, 2002, 2005). According to this hypothesis, the dominant hemisphere is specialized at processing information related to movement dynamics, and the non-dominant hemisphere specializes in processing information on the velocity and position of the limb. Hence, such specialized motor control mechanisms of each hemisphere contribute to the control of both arms during the movement. These characteristics have been demonstrated in multiple studies that directly compared the behavior of the dominant arm and the non-dominant arm during rapid targeted reaching movements (Sainburg & Kalakanis, 2000), adaptation to added masses (Sainburg, 2002), and visuomotor adaptation (Sainburg & Wang, 2002).

Previously, the advantage of the dominant arm was investigated through the mass adaptation paradigm (Sainburg, 2002). Sainburg asked participants to make a point-to-point reaching movement from a central position to eight surrounding targets (a center-out reaching task). Participants were perturbed by an extra load attached to the forearm, which created novel interlimb dynamics. With this type of perturbation, participants needed to learn to control the novel interlimb dynamics created by the extra load to regain their baseline performance. The experiment was composed of three blocks of trials: The first block was pre-exposure for the baseline performance; the second was mass-exposure for the adaptation process; and the last was post-exposure to measure the aftereffect. In this paradigm, the motor lateralization model predicted a better adaptation to novel interlimb dynamics in the dominant arm. The linearity of the hand trajectory and the accuracy of the final position were measured to assess the movement. Both arms showed a similar time course for adaptation, but the dominant arm demonstrated better adaptation than the non-dominant arm in the movement linearity. The dominant arm also showed a better final position accuracy, relative to the baseline performance, than the non-dominant arm showed (Figure 4B). This result suggests that the dominant arm has an advantage in predicting task dynamics and controlling interlimb dynamics in a multi-joint reaching movement.

The distinct advantages of the dominant arm and the non-dominant arm in a reaching movement were demonstrated in a study of rapid targeted reaching movements by (Sainburg & Kalakanis, 2000). In this study, participants performed a rapid reaching movement toward targets in three different directions requiring distinct limb dynamics. The results showed no difference between arms in final position accuracy across the targets. However, the linearity of the hand

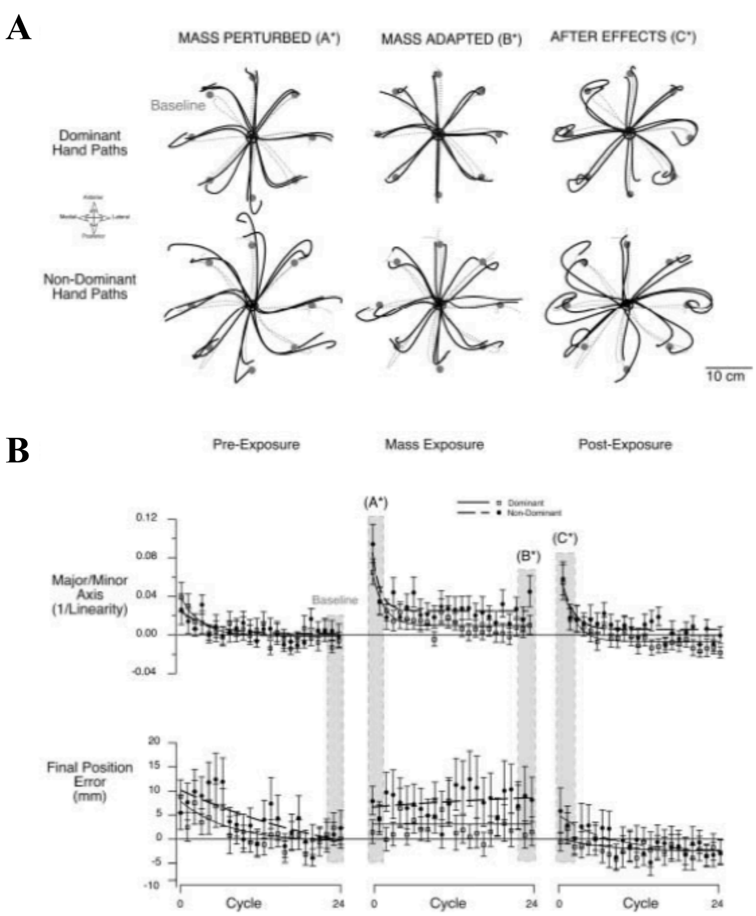


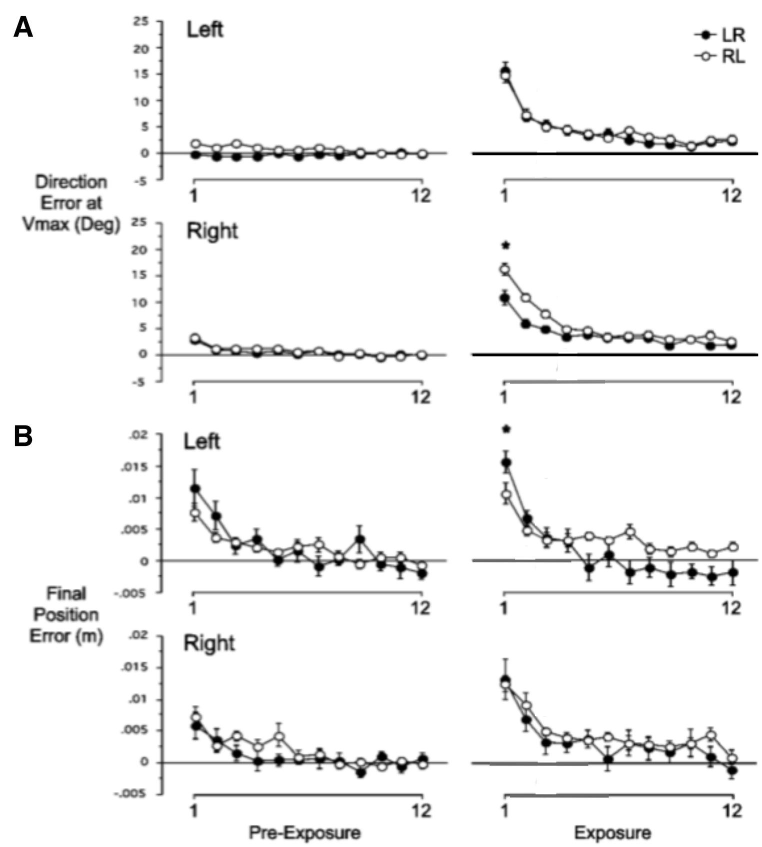
Figure 4 Results from the experiment of Sainburg **A:** Representative hand trajectories from one participant in each arm. Hand trajectories at the end of baseline block were drawn in a light gray color, and the hand trajectories during the perturbation block were drawn in a black color. **B**: Mean performance, the linearity and the final position, from all participants in both arms during each block of experiment. Each cycle contains the averaged measure of eight trials towards targets in every direction. This figure is directly adapted from the original article (Sainburg, 2002).

trajectory toward every target was consistent when participants used the dominant arm, but was systematically different across all targets when the non-dominant arm was used. With the non-dominant arm, hand trajectories toward the target that require more coordination of the shoulder and elbow joints showed more curvature than the hand trajectories that require comparatively simpler coordination of joints. Results of inverse dynamics analysis showed that the dominant arm made use of the interaction torque, the torque generated by the movement of linked segment, created from torques at the shoulder and elbow joint, while the non-dominant arm did not make use of this interaction torque. However, despite the difference between arms in joint coordination strategy, both arms demonstrated the same final position accuracy. This result suggests that the dominant arm has the advantage in controlling interlimb dynamics and the non-dominant arm has the advantage in stabilizing movement at the specified location.

Interlimb transfer of learning

Interlimb transfer of learning has been commonly thought of as a process resulting from shared information between the two hemispheres of the brain. Some adaptation learning studies have found that the information learned in one arm could be accessed by the opposite arm during task performance, which demonstrates the effect of opposite-arm training (Criscimagna-Hemminger, Donchin, Gazzaniga, & Shadmehr, 2003; Sainburg & Wang, 2002; Wang & Sainburg, 2004). Sainburg and Wang (2002) proposed that access to the information stored through opposite-arm training depends on the properties of the controller that is retrieving the opposite-arm driven information. In this study, right-handed participants were asked to perform the center-out reaching movement task under a 30° visuomotor perturbation. One group of participants (RL) performed the task initially with the dominant arm and later with the non-dominant arm, and another group (LR) performed the task in reverse order. The task performance of the dominant arm in one group and the task performance of the non-dominant arm in the other group were compared to investigate the effect of opposite-arm training. The final position error and the initial direction of the hand (when the hand velocity reached its peak) were measured. It is important to note that the final position error is determined by sensorimotor error correction during movement, and the initial direction of the hand reflects predictive control. In the initial performance, both arms showed very similar adaptation profiles for the direction error and the final position error. However, the effect of opposite-arm training in the non-dominant arm showed a reduction in the final position error and invariance in the direction error, whereas the same training in the dominant arm produced a reduction in the direction error but not in the final position error (Figure 5). This result demonstrates that initial training with the dominant arm helped the non-dominant arm to achieve better final position accuracy, whereas the non-dominant arm helped the dominant arm to achieve better initial direction. This suggests that one hemisphere could access the information built from the opposite hemisphere based on its specialized control

Figure 5 Results from the experiment of Wang and Sainburg. Direction error and final position error in both groups. Each dot represents the mean value across the participants in each group (LR and RL group). Each row shows the graphs of labeled hand in both groups. Error bar indicates the standard error. **A**: Direction error vs. cycles of trials graph for the pre-exposure (baseline) and exposure condition. **B**: Final position error vs. cycles of trials graph for the pre-exposure (baseline) and exposure condition. This figure is directly adapted from the original article (Sainburg & Wang, 2002).



mechanism. The dominant controller could retrieve information about the initial direction from the non-dominant controller, and the non-dominant controller could retrieve information about the final position from the dominant controller.

Motor learning studies that address interlimb differences in motor control are generally make use of adaptation learning paradigms. However, it is not known how lateralization of motor control would emerge during a skill-learning task. Anecdotal experience suggests an influence of lateralization on skill learning, but there is little evidence of a similar degree of influence on adaptation learning.

The current experiment

Previously, John et al. (2016) studied a 1-D virtual shuffleboard task in which the puck was constrained to move along a straight line. Detailed description of the task and task variables are discussed in the previous paragraph. In this task, participants started each movement at a fixed starting location and attempted to place the puck on a fixed target in one direction. The puck is released by the participant, and a distance the puck travels depended on two task variables at the moment of release. They could freely choose the task variables, release distance (x) and release velocity (v), that lead to achieve this goal. While this task allowed participants to have redundant solutions at the task level, the level that yields task performance via a mathematical definition, the player's movement of an end effector itself was restricted to 1-D space. We now define a new shuffleboard task in a 2-D space that allows two levels of redundancy: A participant can choose the strategy to impact the puck, and can also choose the strategy to initiate the movement. In this 2-D shuffleboard task, participants have redundancy at the task level, which happens at the puck impact, that determines the task performance and another redundancy at the body level that allows players to initiate the movement at their biomechanical preference. Different from 1-D shuffleboard task, our current task allows higher degrees of freedom at the body level since now the end-effector movement is on 2 dimensions. For example, the task can be performed entirely by a single-joint movement or it can be performed by a multi-joint movement with different contributions of shoulder and elbow joints. This design makes the task more resemble our daily activities. This substantial redundancy embedded in the task, allowing infinite solutions along a task manifold, provides alternative solutions that might reflect the control strategy in coordinating the variables for achieving a goal during task performance.

In this experiment, we articulated three research questions addressing the effect of lateralization, the control strategy of the redundant system, and the effect of opposite-arm training on a skill-learning task. The 2-D shuffleboard task has two main components characterizing skill learning, as opposed to adaptation learning. First, this is not a task that individuals perform accurately when first exposed to it. Instead, experience leads to improvements beyond the pre-trained level of performance. Second, there are no perturbations, such as externally imposed forces or unusual visual feedback, that create a deviation from baseline performance, as is the case for adaptation tasks.

We tested three hypotheses in this experiment. First, we hypothesized a motor lateralization model, that attributes predictive control to the dominant hemisphere and impedance control to the non-dominant hemisphere. In the 2-D shuffleboard task, players make a rapid movement to strike the puck, and the impact happens when the hand velocity reaches its peak. To hit the target, participants must strike the puck with the correct estimation of peak hand speed and initial direction of hand trajectory that leads to the goal. Therefore, we predict the dominant arm will show better performance than the non-dominant arm by utilizing its predictive control advantage. Second, we hypothesized that the CNS exploits the given set of redundancies to maintain skill level, that is once learning was completed. We predicted that participants will exhibit large variability in the redundant space at the task-level and at the body-level as a sign of exploiting redundancy. Lastly, we hypothesized that each hemisphere retrieves information from the other based on its control specialization. In our task, precise predictive control of hand speed and hand trajectory direction is critical for the task success. However, control of limb posture seems to be less important in our task since the movement after puck impact doesn't contribute to the task success. Thus, we predict that the dominant arm after the training with the non-dominant arm will show better transfer of learning compared to the non-dominant arm after the training with the dominant arm. This prediction is based on the modified access model which suggests that the opposite arm driven information is retrieved based on the properties of the controller. The dominant arm after the non-dominant arm training will exhibit improvement in task performance by retrieving information about its specialized predictive control which seems to be critical for achieving the goal in the 2-D shuffleboard task. Also, this improvement will be greater than the non-dominant arm would show after the training with the dominant arm since the non-dominant controller will retrieve information about its specialized limb position control which seems less important for task success.

Chapter 2

Methods

A 2-D redundant shuffleboard task

In the 2-D shuffleboard task, there are three objects, mallet, puck, and target, on a horizontal plane. The mallet is driven by the player, and the task is performed as the player hits the puck with the mallet toward a semicircle shaped target (Figure 6). The puck starts from rest at the origin at the beginning of each trial. A player could choose where to initiate the stroke anywhere inside of the starting box, and one could aim in any direction to the target. The starting box had a width of 0.7 m and a height of 0.1 m, and it was located 0.1 m away from the initial position of the puck. The target was located 0.35 m away from the origin to every 180 degrees of forwarding direction (Figure 6). Freedom to choose movement initiation location and the puck direction offers redundancy at the movement initiation, so it allows the player to perform the task using a range of possible biomechanical strategies. For example, the player could achieve the same task result with different joint configuration by choosing different stroke initiating locations and the puck direction.

After the stroke, the puck launches to a direction along the line of impact, a straight line that crosses the center of mallet and the center of the puck at impact (Figure 6). The puck slides on the plane according to the velocity of mallet at impact and decelerates under the action of Coulomb friction (μ) between the plane and the puck until the puck eventually comes to rest. The task error (e) is defined as the magnitude of distance between the center of the puck at final position and the closest point in the goal line (Blackline of the target). The behavior of the puck after the impact is entirely determined by three variables: (ϕ), the angle at which the mallet impacts the puck; (θ), the heading of the mallet when impact occurs; and (v), the speed of the mallet at impact. The goal of this task is to strike the puck to let it stop at the goal line. Since the target is located in all 180 degrees direction from the origin, participants could achieve the goal in any puck direction within 180 degrees range. Therefore, it reduces the number of relevant task variables to two: ($\phi - \theta$), the deviated angle from the puck direction, and (v) the speed of the mallet. The relationship between two task variables offers redundancy at impact that allows the player to achieve the same goal with many combinations of $\phi - \theta$ and v on any given trial. In the all possible combinations that lead to the goal, we define the optimum mallet speed as the minimum mallet speed that leads to the goal when the heading of the mallet passes straight through the center of the puck, when $\phi - \theta$ *equals zero,* at impact. Therefore, in the 2-D shuffleboard task, there is redundancy at the movement initiation, where you initiate the movement and what direction you aim to, and another redundancy at puck impact built in the task that the player could exploit to achieve the goal.

Blue and red colors of the target indicate the proximity to the goal line with the range of 0.005-0.015m and 0.015-0.025m from the goal line respectively. To reward participants, graded scores and pleasant sounds were awarded to the player at the end of the trial when the player successfully stops the puck on the target. Red, blue, and black colors were worth 1, 3, 10 points respectively. After puck stops, the center of the puck was briefly revealed as a red dot to notify player the final position of the puck. The next trial automatically started as the puck re-appears at the origin. The player was instructed to obtain as high scores as possible throughout the experiment.

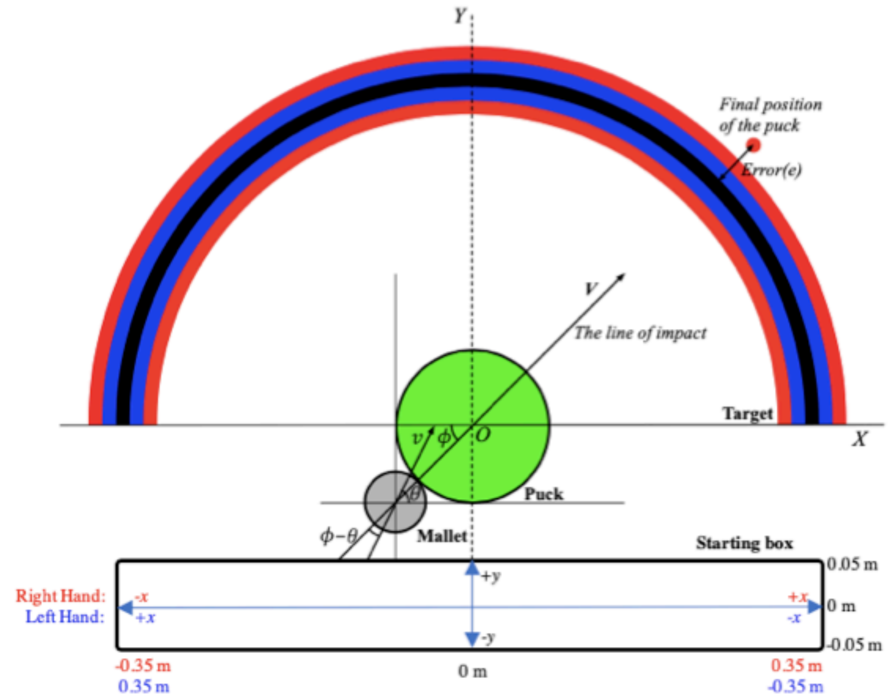


Figure 6 Task definition and coordinate system for impact-based shuffleboard. The task parameter space consists of doubles x = (ϕ - θ, v), representing the deviated angle from the puck direction, and the speed of the mallet, all at impact. After impact, the puck moves with speed V, as determined by the "state" x just before impact. The target is located at a constant distance (0.35m) away from the origin. The center of the starting box is the origin of the coordinate system. From the origin, the Y coordinate is positive towards the top line of the starting box, and it is negative towards the bottom line. From the origin, the X coordinate is positive towards the side of performing arm, and it is negative going further from the side of performing arm. The size of the puck and the mallet is enlarged in this figure than the actual size for the sake of illustration.

Participants and experimental setup

Sixteen healthy adult participants (8 male and 8 female) were recruited for this study. They were all right-handed individuals who were between 18 to 35 years old. The handedness of the participants was determined by the Edinburgh Handedness Inventory with scores of 90% in the inventory(Oldfield, 1971)(Appendix A). Participants were verbally asked to exclude if one reported any history of neurological disorder or upper extremity injuries or participating in sport at a competitive level following a health history questionnaire in the experiment checklist

(Appendix 2). All of the participants signed a written informed consent that was approved by the institutional review board of Pennsylvania State University (IRB #: PRAMS00040722).

All data were collected by the Kinereach system (Figure 7). Participants sat in a chair that was adjusted to each individual's sitting height. A mirror was placed above the table to reflect the screen of an inverted 55" HD digital TV which was located 21 cm above the mirror. Both arms were placed on the air sleds which allows any motion in horizontal plane to be near frictionless. Wrists and fingers movements were restricted by using a splint to simplify the degree of freedom. Fingers were clinched naturally as they hold the splint on the air sleds. A magnetic motion capture system, "TrackStar (Northern Digital Instrument)," was used to track the arm movement. Two of 6 DOF magnetic sensors were attached on the upper arm and on the back of the hand. Then, a total of seven bony landmarks were digitized in the Kinereach system: 1) between proximal phalanx and middle phalanx of index finger; 2) between MCP joint of ring and middle finger; 3) the distal end of the radius; 4) the distal end of the ulnar; 5) the medial epicondyle of humerus; 6) the lateral epicondyle of humerus; and 7) the acromion process. The system recorded the position of these seven digitized points during the movement. In this setup, the mirror blocked the sight of the participants to their arms, but they received the visual feedback of the location of the index fingertip, between proximal phalanx and middle phalanx of index finger, as a form of mallet from the screen in real-time during the task. The movement during the task was captured with a sampling rate of 116 Hz, and arm kinematics were calculated with custom REALbasic (Xojo).

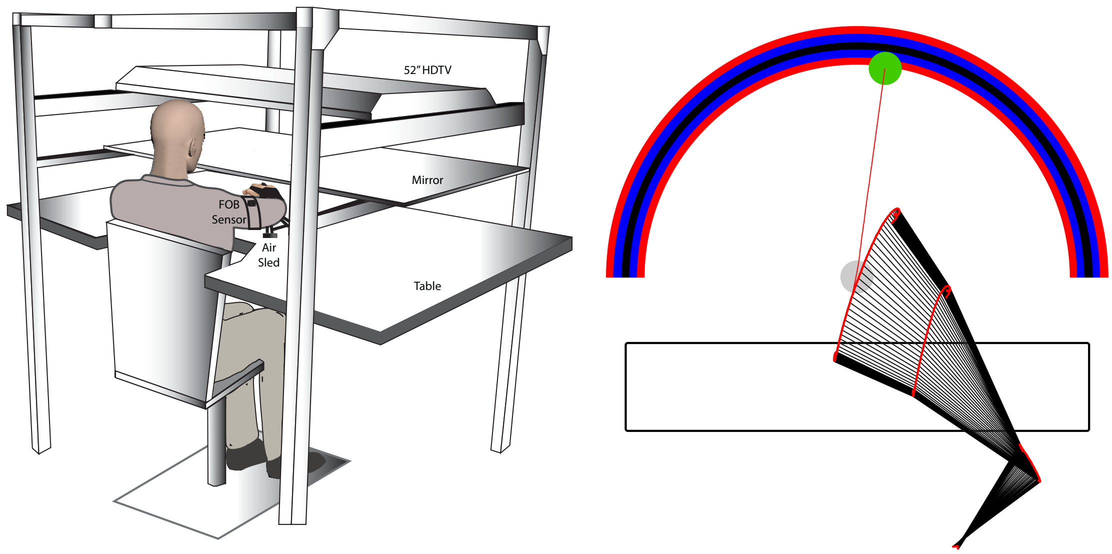


Figure 7 Experiment apparatus. A: Schematics of the Kinereach system. B: Example arm and puck trajectory from a participant from the RL group. The gray circle is the initial position of the puck prior to the impact. The horizontal trajectory of the shoulder, elbow, wrist, and fingertip during the movement, from the movement initiation to the end of the movement, are illustrated. All positions at each time are connected by a black line. The green circle is the puck after it slides according to the task variables (ϕ - θ, v) at impact.

Experimental protocol

We assigned participants into two groups that each group performs the task with a different order of arms. Eight participants (4 males and 4 females) were assigned to the RL group, which performed the task in the dominant to non-dominant arm order. The other eight participants (4 males and 4 females) were assigned to the LR group, which performed the task in the reverse order. The experiment was composed of 4 sessions in two consecutive days, and each session was composed of 300 trials. On the first day, participants performed the task for two sessions with the assigned arm in each group. On the following day, 24 hours later, participants re-visited the lab to complete the third session and the transfer session. In the third session, participants performed the task with an identical arm as the previous day. They then performed the task with the opposite arm in the transfer session. Throughout the experiment, a 5-minute break was given between the sessions (Figure 8).

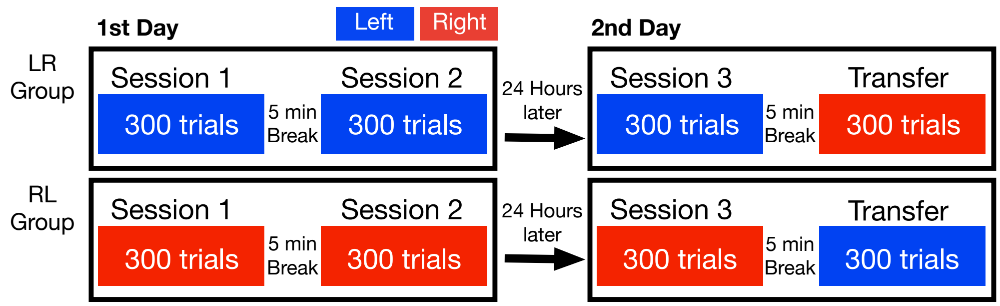


Figure 8 Timeline of the study. LR group and RL group performed the 2-D shuffleboard task with a different order of arms. Each session was composed of 300 trials, and participants had a 5-minute break in between sessions. Visit on the second day was scheduled approximately 24 hours after the first session.

Kinematic data

All of the positions of the digitized bony landmarks on the upper limbs were calculated from the sensor data collected from the Kinereach system. Kinematic data were low-pass filtered at 8 Hz using 3rd order dual-pass Butterworth filter, and filtered position data were differentiated for tangential velocity and acceleration values. The start of movement was determined as the moment before the tangential velocity of the fingertip (the mallet) reached its peak when the tangential velocity of the index finger was below 6% of the peak tangential velocity of the same trial. The end of movement was determined in a similar way as the movement start, but it was the moment when index finger tangential velocity decreases below 6% of the peak tangential velocity after the moment of peak tangential velocity.

Dependent measures and analyses

Task learning

We quantified how participants learned the task by calculating task error (*e*) in session 1 and session 2. Task error was calculated by taking a magnitude of distance between the center of puck at the final position and the closest point in the goal line. We took the magnitude of task error rather than signed task error to focus our measure on how participants reduce the error. Whether the puck was overshooting and undershooting in the course of error reduction was not our major focus. In every analysis of this study, we organized the trials as follows. Each session consisted of 300 trials. We organized these into 15 epochs, with each epoch containing 20 consecutive trials. The number of trials in each epoch was decided for our convenience in the data analysis, and we confirmed that our conclusions are invariant regardless of the composition of the epoch. The within-participant mean and within-participant standard deviation of task error for each participant (N=16) in every epoch of session 1 and 2 were calculated. The mean and the standard errors of these values across the participants in each group (RL and LR group) were calculated for each epoch and plotted against epoch (1-30). The standard deviation and standard error indicate two different values. The standard deviation is the measure of variability from the mean, and the standard error is the measure of how the sampled mean close to the true mean. We fitted a second term exponential fit to the graph to show a general trend of the change of the mean and standard deviation of task error. As a sign of learning, we expected to see a significant reduction in the mean and standard deviation of task error over epoch (Muller & Sternad, 2004; Todorov & Jordan, 2002). For statistical analysis, we performed 3 factor (subject, hand, epoch, hand*epoch) mixed effect analysis of variance (ANOVA) on the mean and standard deviation of task error. Hand (right vs. left), epoch (1~30), hand*epoch were the fixed factor and subject (n=16) was the random factor in the analysis. This analysis could be called as the repeated measures ANOVA since the same dependent variables were being measured from the same participants repetitively throughout the session. For the post-hoc analysis, we performed the Tukey comparison test on epoch factor to check the change of dependent variables between epochs.

Learned task performance – movement initiation

For the task performance analysis, we decided to analyze session 2 where the task performance and variability plateau at the low level to the end. In the post-hoc analysis, Tukey comparison test of epoch factor on the mean and standard deviation of task error in session 2 revealed no significant effect of epoch. Lack of statistically significant change in the mean and the variability of task performance suggests the completion of learning, so we used data in session 2 to examine how participants learned to exploit the redundancy embedded in the task. We measured the location of the mallet at the movement initiation and the puck direction (ϕ) to examine where participants chose to initiate the movement after they learned the task. We calculated the within-participant mean and within-participant standard deviation of the movement initiation location (X and Y coordinates) and the puck direction (ϕ) in session 2 for each participant (N=16), and these values were plotted as a box plot separately by hand. The movement initiation location inside of the starting box was analyzed in a plane cartesian coordinate system that has x and y coordinates. In this coordinate system, the center of the starting box is the origin. The y coordinate is positive going forward towards the top border of the starting box from the origin, and it is negative towards the bottom border of the starting box from the origin. The X coordinate is positive towards the side of performing arm from the origin, and it is negative going away from the side of performing hand from the origin. The puck direction (ϕ) was defined as the angle measured between the lateral line of the horizontal axis of the performing arm to the line of impact. The line of impact is a line that connects the center of the mallet and the center of the puck at impact. The puck direction (ϕ) was calculated between the position of the mallet at the impact and the position of the mallet captured 8.6 ms before the impact. For statistical analysis, we performed one-way ANOVA that includes a single factor (hand) on the mean and within-participant standard deviations of the movement initiation location and the puck direction in session 2 to compare between hands.

Learned task performance – puck impact

We examined how participants chose the task variables at impact as a result of task learning by comparing the deviated angle from the puck direction ($\phi - \theta$) and the speed of the mallet at the impact (v) of both groups. The heading of mallet (θ) was defined as the angle measured between the lateral line of horizontal axis of the performing hand and the vector direction of the center of the mallet at impact. The deviated angle from the puck direction ($\phi - \theta$) was calculated by subtracting the heading of mallet (θ) from the puck direction (ϕ). The speed of mallet (v) was measured right before the impact happened. All of the task variables at impact, the deviated angle from the puck direction ($\phi - \theta$) and mallet speed (v), were calculated between the position of the mallet at the impact and the position of the mallet captured 8.6 ms before the impact. We calculated the within-participant mean and within-participant standard deviation of these task variables from each participant (N=16) in session 2. The calculated values were plotted as a box plot against hands. For statistical analysis, we performed one-way ANOVA that includes a single factor (hand) on the mean and within-participant standard deviations of $\phi - \theta$ and v to compare between hands.

Retention of learning

The extent of learning retained after 24 hours was examined by comparing the task error in session 1 and session 3. We compared the first epoch of session 1, the naïve state without a previous training, to the first epoch of session 3, the learned state with a training from day 1. For each participant (N=16) in both groups, we calculated the within-participant mean and within-participant standard deviation of task error in every epoch of session 1 and session 3. The mean and the standard error of these values were calculated across the participants in each group, and these were plotted against the epoch. Also, the same values of the first epoch in session 1 and session 3 were plotted as box plots for both hands group. As a sign of retention, we expected to see a significant reduction in the mean and standard deviation of task error in the first epoch of session 3. For the statistical analysis, 3 factor (subject, hand, day, hand*day) mixed effect ANOVA was conducted on task error data of the first epoch in session 1 and 3. Hand (right vs. left), day (naive vs. 24 hours later), and hand*day were the fixed factor, and subject was the random factor in the analysis.

Interlimb transfer of learning

The effect of the opposite-arm training was tested by comparing the initial task error of one arm in a group to the task error of the same arm, after training with the opposite arm, in the opposite group. For each participant in both groups, we calculated the mean and within-standard deviation of task error in every epoch of session 1 and the transfer session. The mean and the standard error of these values were calculated across the participants in each group, and these values were plotted against epoch for both hands group. The within-participant mean and within-participant standard deviation of task error in the first epoch of session 1 and the first epoch of the transfer session were compared as these epochs respectively represent the naïve state and the state after the training with the opposite arm. These values were plotted as box plots for both hands. As a sign of interlimb transfer of learning, we expected to see a significant reduction in the mean and standard deviation of task error in the first epoch of the transfer session. For statistical analysis, we performed 2 factor (hand, training, hand*training) fixed-effect ANOVA on task error data of the first epoch on session 1 and the transfer session. Hand (right vs. left), training (naive vs. opposite-arm training), and hand*training were included as the fixed factors in the analysis. The data from one participant in the RL group who failed to follow the instructions in the transfer session was excluded from the analysis.

Chapter 3

Results

Task learning

Participants in both groups learned the task throughout the session 1 and session 2. During practice in session 1 and session 2, both groups showed significant reductions in the mean and SD of task error. Regardless of the group, the mean task error decreased rapidly during the first three epochs of session 1, and then the reduction slowly plateaued after epoch 4 to the end of session 2 (Figure 9A). The 3 factor mixed-effect ANOVA result showed a significant effect of epoch ($P < 0.0001$), and following Tukey pairwise post hoc comparison on epoch factor revealed that the mean task error decreased significantly until epoch 4 and plateaued after epoch 4. After epoch 4, there was no statistically significant change in mean task error until the end epoch of session 2. Regardless of the group, the SD decreased rapidly during the first three epochs in session 1 and slowly plateaued from epoch 4 to the end epoch of session 2 (Figure 9B). The statistical analysis showed that there was a significant effect of epoch ($P < 0.0001$). In addition, Tukey pairwise post hoc comparison on epoch factor showed that the SD of task error decreased significantly during the first three epochs in session 1, but there was no significant change in SD of task error after epoch 4. These statistical results of the mean and SD of task error suggest that most of learning of task occurred at the beginning of session 1 and the learning occurred in a slow pace after epoch 4 to the end of session 2 as the reduction in the mean and SD of task error plateaus.

There was no statistical difference between hands in learning of task. Both groups showed a similar learning curve during the rapid reduction of the mean and SD of task error in the early epochs of session 1, and both groups showed a similar extent of learning (Figure 9). There was not enough statistical evidence to conclude difference between hand groups in the mean and SD of task error. The 3-factor mixed-effect ANOVA for the mean task error and the SD of task error showed non-significant effects on hand factor, the mean task error ($P = 0.11$) and the SD of task error ($P = 0.198$). These results demonstrate that the task was learned symmetrically with a similar time course regardless of the performing hand.

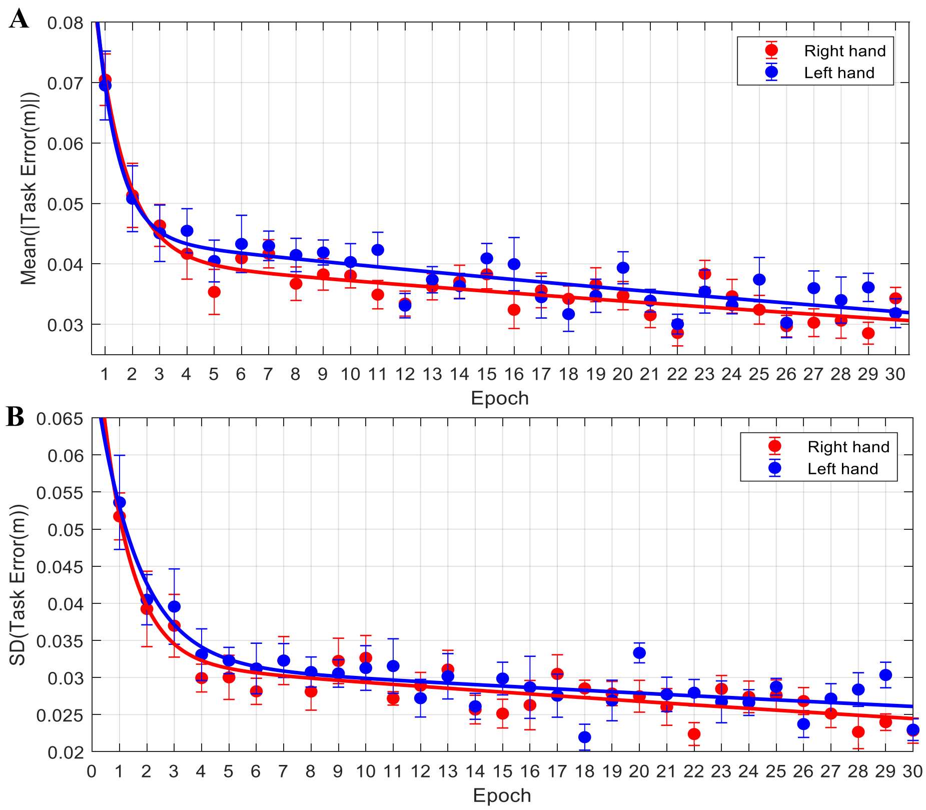


Figure 9 Task performance results in sessions 1 and 2 for both groups. A: Mean of task error (m) vs. epoch graph B: Within participant standard deviation of task error vs. epoch graph in sessions 1 and 2. Each data point was averaged across participants in each group. The error bars indicate the standard error of the mean. For both groups, the mean and the within-participant standard deviation of task error decreased significantly at the beginning and stayed around the same level after epoch 4.

Learned Task Performance – Movement Initiation

After the participants mostly learned the task in the early epochs of session 1, they maintained the statistically similar task performance throughout the session 2. The movement initiation location data in session 2 showed that the participants were starting the movement at the similar location in the starting box regardless of the performing hand. Both groups showed a very similar aspects when selecting a movement initiation location (Figure 10). In x coordinates, on average, the right-hand group initiated the stroke from the center of the starting box. On average, the left-hand group also initiated the stroke from the center of the starting box. For both groups, the individual participant mean data were clustered at the center of the starting box (Figure 10A). In y coordinates, on average, both groups initiated the stroke from the upper portion of the starting box. The individual participant mean data for both groups were clustered in the upper

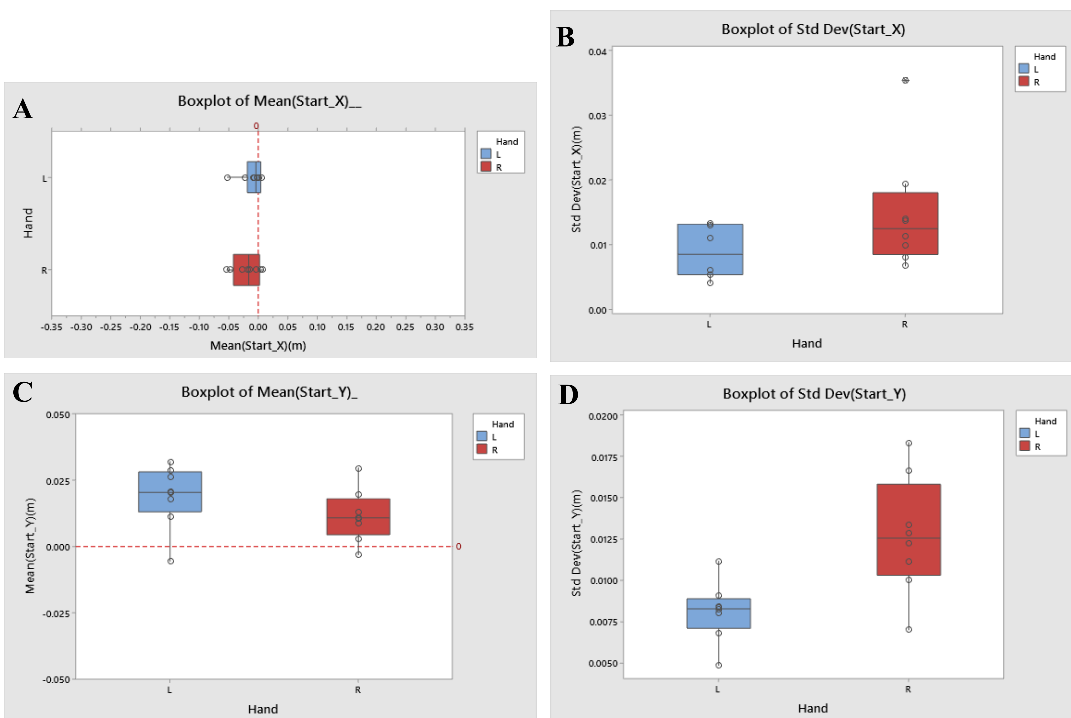


Figure 10 Mean and standard deviation of movement initiation location in session 2. A and B: a boxplot of the mean and standard deviation of x coordinate of movement initiation location. For A, a negative value indicates the further side of the starting box when a positive value indicates the closer side of the starting box from the side of the hand. C and D: a boxplot of the mean and standard deviation of y coordinate of movement initiation location. The empty dots indicate the individual mean data in session 2. The dotted line denotes the middle line of the starting box. Both groups initiated the stroke from the middle upper side of the starting box.

portion of the starting box (Figure 10C). The one-way ANOVA revealed that there was no significant hand difference in the mean x coordinates ($P = 0.319$) and y coordinates ($P = 0.228$). Moreover, participants in both groups showed the similar standard deviation of movement initiation location in x and y coordinates. The one-way ANOVA on the SD of the movement initiating location showed that there was no significant hand difference in x coordinates ($P = 0.129$) and y coordinates ($P = 0.161$). Overall, on average, participants in both groups initiated the movement from the center at the upper side of the starting box, and they had similar variability when choosing the starting location regardless of the performing hand.

When participants performed the task, they were able to choose a direction when they aim the target that covers 180° in the forward direction. The participants for both groups struck the puck in the similar mean direction with the similar standard deviation (Figure 11). On average, participants in the left-hand group struck towards about 90 degrees except one participant who struck toward about 65 degrees. Participants in the right-hand group showed more spread mean puck direction ranging from 90 degrees to 65 degrees (Figure 11A). The SD of the puck direction were very similar between hands, both groups showed the standard deviation of 10° to 17° from the mean (Figure 11B). The one-way ANOVA indicated that there was no significant hand difference in either the mean puck direction ($P = 0.180$) or the standard deviation

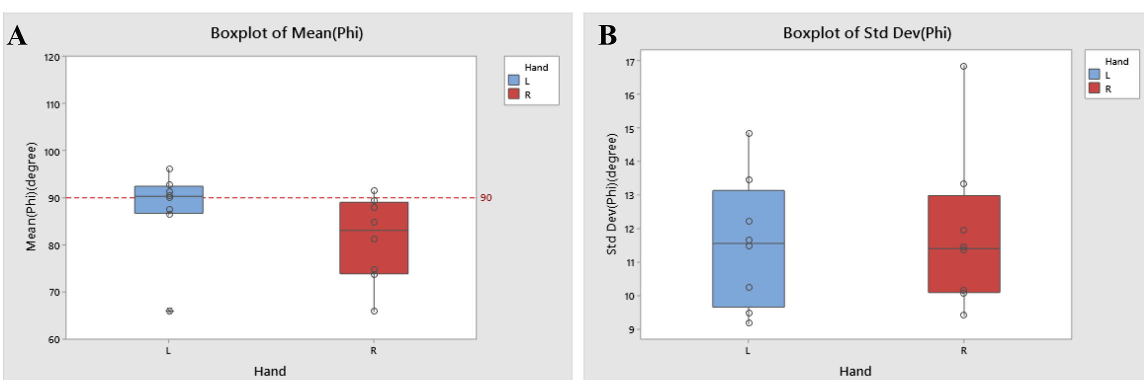


Figure 11 The mean and standard deviation of puck direction in session 2. A and B: boxplots of the mean and standard deviation of puck direction. The dotted line in A indicates the middle of the target (90°), and the empty dots indicate individual mean data in session 2. On average, both groups aimed toward the middle of the target with the similar standard deviations.

(P = 0.813). In summary, after they learned the task, both groups aimed in the forward direction that is close to 90° to the target, and they showed the similar variability.

Learned Task Performance – Puck Impact

When the mallet approaches the puck, task performance was determined by the task variables (ϕ - θ and v) at the impact. On average, participants for both groups exhibited the median mallet speed near the optimum mallet speed, the minimum hand speed that achieve the goal when ϕ - θ equals zero (Figure 12). One-way ANOVA revealed that there was no significant difference between hands in the mean hand speed (P = 0.187) and standard deviation of the hand speed (P = 0.100). Therefore, after the participants learned the task, they chose the hand speed near the optimum hand speed regardless of the performing hand. For the deviated angle from the puck direction, ϕ - θ, participants chose to restrict ϕ - θ close to zero. On average, participants were striking the puck nearly straight through the center of the puck. There was no significant

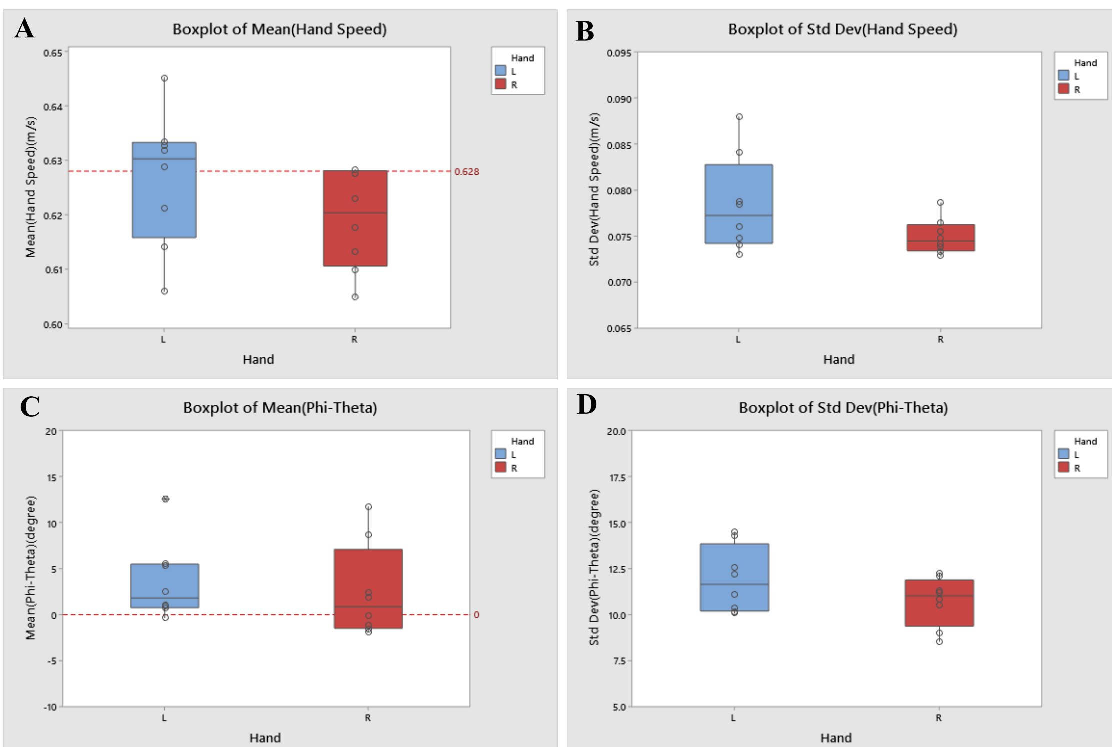


Figure 12 The mean and standard deviation of hand speed and ϕ - θ in session 2. A and B: boxplots of mean and within-participant standard deviation of hand speed at impact. The dotted line in A indicates the optimum hand speed to the goal when ϕ - θ equals to zero. C and D: boxplots of mean and within-participant standard deviation of ϕ - θ at impact. The empty dots indicate individual mean data in session 2. On average, both groups were aiming toward the middle of the target.

difference between hands in the mean and standard deviation of ϕ - θ (Mean: $P = 0.657$ and SD: $P = 0.156$). Overall, on average, participants in both groups made a straight stroke movement that goes through the center of the puck with the hand speed near the optimum hand speed. Also, the extent of variability was similar between the hands.

Retention of learning

Participants in both groups showed improved task performance when they returned 24 hours after the initial training. For both groups, participants showed the reduced mean task error throughout the session 3 compared to the mean task error in session 1 (Figure 13AB). In the comparison between the first epochs of session 1 and session 3, the mean and the standard deviation of task error were significantly reduced in the first epoch of session 3 (Figure 13CD). The result of 3 factor mixed effect ANOVA on the mean and the standard deviation of task error showed that there was a significant difference in epoch factor (naïve vs. 24 hours later) with p-value less than 0.0001 for the mean and with p-value less than 0.001 for the standard deviation. On the other hand, there was no significant difference between hands in the extent of reduction of the mean and standard deviation of task error (Mean: $P = 0.967$ and SD: $P = 0.613$). Therefore, for both groups, participants retained the task learning after 24 hours from the initial training.

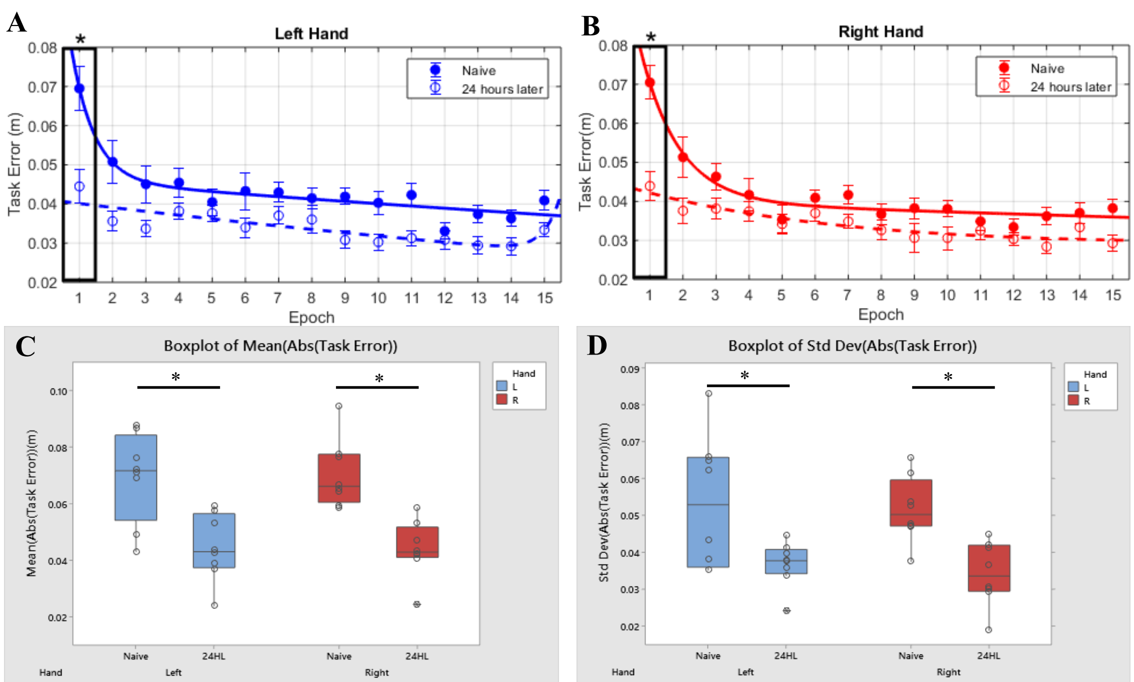


Figure 13 Retention of learning over 24 hours for both groups. A and B: the mean task error in session 1 and session 3 are plotted against epoch for the left-hand group and the right-hand group. Error bars denote the standard error of the mean. The data points were fitted with a second term exponential fit. Each data point is averaged value across the participants in each group. C and D: boxplots of the mean and the within standard deviation of the task error at the first epoch in session 1 and session 3 for both hand groups. Each empty dot denotes the individual mean data.

Interlimb transfer of learning

In both hands, participants demonstrated the reduction of mean task error after the opposite-arm training (Figure 14AB). For both hands, in the comparison between the naïve epoch and the epoch with the opposite-arm training, the mean task error and the SD of task error were significantly decreased in the transfer session compare to the mean task error and SD of task error in session 1 (Figure 14CD). The 2 factor fixed effect ANOVA on the mean and SD of the task error revealed the significant effects of opposite-arm training (Mean: $P < 0.001$ and SD: $P = 0.015$). However, there was no significant difference between the hands in the extent of learning transfer from one arm to the other arm. The ANOVA results on the mean and standard deviation of task error showed that there was no effect of hands. (Mean: $P = 0.929$ and SD: $P = 0.739$).

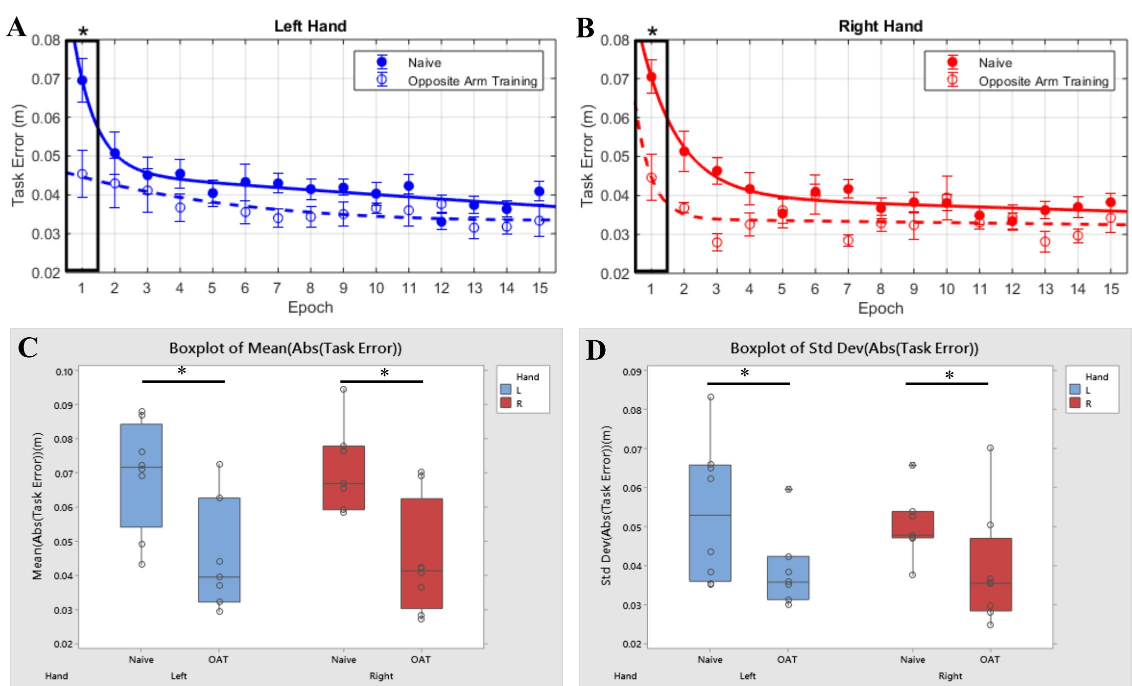


Figure 14 Interlimb transfer of learning in both arms. A and B: the mean task error in session 1 and session 4 was plotted against epoch for both hand groups. Filled data point indicates the mean task error of assigned hand, and the empty dots indicate the mean task error of assigned hand after the opposite-arm training. Error bars denote the standard error of the mean. The data points were fitted with a second term exponential fit. Each data point is averaged across the participants in each group C and D: boxplots of the mean and the within-participant standard deviation of the initial task error for both hands in the naïve and opposite-arm training conditions. Each empty dot denotes the individual data

Chapter 4

Discussion

The current study was designed to test three experimental hypotheses on a skill-learning task. First, we examined the model of motor lateralization, which hypothesizes a distinct aspect of the motor control mechanism in each hemisphere. According to this model, the left hemisphere is specialized at predictive control of movement, which includes coordinating the intersegmental dynamics to the environmental dynamics; the right hemisphere is specialized at impedance control of movement, which stabilizes the limb at the specified location (Mutha et al., 2012; Sainburg, 2002, 2005; Schaefer, Haaland, & Sainburg, 2009). Our experiment focused on testing the control advantage of the dominant controller through a skilled task designed to be proficient in the dominant controller. Second, we tested a hypothesis that the CNS exploits redundancy to maintain a skill level. Lastly, we tested the hypothesis of interlimb transfer of motor learning, i.e., that each hemisphere accesses a specific aspect of motor memory from the other hemisphere based on its specialization in the motor control mechanism (Wang & Sainburg, 2003, 2006).

To test these hypotheses, we devised the 2-D redundant shuffleboard task, which has the characteristics of a skill-learning task, and which offers redundant solutions to achieve a goal. Following the model of motor lateralization, we predicted that the dominant arm will show better task learning and task performance than the non-dominant arm. Also, we predicted that the redundancy embedded at the movement initiation and the puck impact would be exploited once the learning is completed. For the interlimb transfer hypothesis, according to the modified access model, we predicted enhanced initial task performance in the dominant arm after training with the opposite arm, but not so much improvement in the non-dominant arm after training with the opposite arm.

In task learning, our findings did not support our first hypothesis. The dominant and non-dominant arms showed very similar task learning and performance. With regard to the exploitation of redundancy, our second hypothesis was not supported. Both arms showed limited range of exploitation in the redundant space at the movement initiation and at the puck impact after the skill level was plateaued. Our last hypothesis was not supported, as substantial interlimb transfer of learning occurred in both directions—from the dominant arm to the non-dominant arm and vice versa.

Exploiting redundancy in a 2D redundant shuffleboard task

In this task, task performance is solely determined by two task variables at task level: the hand velocity (v) and the deviated angle (ϕ - θ), at impact. When the ϕ - θ was zero, the goal could be achieved with the minimum hand velocity. As the magnitude of ϕ - θ increased, greater hand velocity was required to achieve a goal, since only a component of hand velocity transfers to the puck direction. Furthermore, participants were free to choose the movement initiation location anywhere inside the starting box. Therefore, they were allowed to perform the task with infinite combinations of task variables, and they were allowed to perform the task with the movement at their biomechanical preference. Such redundancy at task level and at body level allowed us to test how people exploit these during the performance of a skilled task.

Our findings demonstrate that, on average, participants in both groups didn't exploit the redundancy at both levels. Instead of taking advantage of infinite strategies, they performed the task with a limited range of strategies when selecting task variables and movement initiation location. Among all of the choices, on average, participants selected to start the movement from the upper center of the starting box. In the puck impact, participants selected the ϕ - θ at near zero and hit the puck with a hand speed that is close to the optimum hand speed. This strategy at puck impact led the puck in a nearly 90° direction. For both arms, the mean and variability of these variables were not significantly different. Participants in both groups didn't exploit the redundancy. They rather selected to perform the task with the consistent strategy after learning was completed.

This finding suggests that there might be some kind of advantage at not exploiting redundancy when performing this task. This advantage might arise from both biomechanical and neuromuscular reasons. For biomechanical reason, participants might have found a strategy to stabilize the hand trajectory in a linear shape to increase accuracy when executing a planned hand trajectory. By repeating the movement from one starting location that yields the best possible accuracy, they maintained the skill level. On the other hand, exploiting redundancy at the starting box would force participants to learn different limb dynamics, and this will impose more control effort when trying to maintain the accuracy of the movement. For neuromuscular reason, participants can perform the task with less difficulty when hitting the puck with the least ϕ - θ and the optimum hand speed. To produce higher speed movement, the greater amount of motor units is recruited, and it yields larger noise in the course of force generation which could disturb the movement accuracy. Therefore, it is possible that participants performed the task with the least ϕ - θ and the optimum hand speed to prioritize the movement accuracy which directly related to task performance. For that reason, strategies with higher ϕ - θ and higher hand speed would make the task more difficult for participants. These reasons might have led participants not to exploit redundancy since exploiting redundancy would bring disadvantages at improving task performance.

Our original plan to analyze the variability by plotting these variabilities in a task manifold was not fulfilled in the current experiment, due to time constraints. Therefore, it is not possible at the current stage to answer our original question of how these variabilities are temporally and geometrically structured in a task manifold by the trial-to-trial error regulation process.

The effect of motor lateralization on a skill-learning task

In the performance of the 2-D shuffleboard task, participants made a rapid straight movement from the starting box to hit the puck at the peak velocity. In this movement, the hand reaches its peak velocity in a very short time, so we assume the controller to rely on the feedforward control to perform this task. Therefore, we predicted that the dominant arm would outperform the non-dominant arm in this task followed by the model of motor lateralization. In the task that was designed to be advantageous for the dominant controller, interestingly, our findings showed that the dominant and non-dominant arms exhibit a very similar time course of learning and extent of learning. These results were different from our prediction, and the hypothesis of motor lateralization was not supported. The lateralization of control mechanism didn’t emerge in our task, and this contradicts what has been demonstrated in previous adaptation studies and reaching studies. We suggest that the non-dominant controller is able to build the predictive control model as much as the dominant controller does. This was demonstrated in our results which showed symmetrical task learning and performance in both controllers.

This symmetry in task learning and performance might be due to the similarity in the movement strategy. As just described, movement initiation location and puck impact data showed that very similar strategies were used in both arms. Both arms maintained the low task error while performing the task with near optimum hand speed with the smallest ϕ - θ from the center of the starting box. In most of the participants’ performance, individual hand trajectories were very similar for both arms (Appendix D). The movement learned from this strategy might have led the controllers to perform the task mostly with elbow joint movement. It is possible that the effect of motor lateralization was washed out because the movement was equally performed in both arms in a way that does not require high intersegmental coordination. Given previous evidence that the advantage of the dominant arm is prominently revealed in movements with high intersegmental dynamics, it is plausible that both arms were able to perform this task symmetrically if the movement was performed with low intersegmental dynamics. The symmetrical task performance in such movement was demonstrated in the previous study with a single elbow joint reaching movement (Sainburg & Schaefer, 2004) and in the study with a multi-joint reaching movement (Sainburg & Kalakanis, 2000). In the Sainburg and Schaefer study, participants made the elbow joint reaching movement to targets in linearly different distances with either the dominant or non-dominant arm. The result indicated that the peak tangential velocities and the final position accuracies for every target were symmetrically demonstrated in both arms. Furthermore, in the Sainburg and Kalakanis study, participants performed a multi-joint reaching movement to the targets that elicited different interaction torques at the elbow joint. The initial direction accuracy in both arms was symmetric in the movement made toward a target that required the least interaction torque. The movement was performed mostly with the elbow joint. These results suggest that both arms control the direction and the velocity to a similar extent when the movement is mostly performed with the elbow joint. However, further analysis is necessary to confirm whether the learned movement was indeed performed with low intersegmental dynamics.

Interlimb transfer of motor learning based on the modified access model

In the visuomotor adaptation learning experiment, Wang and Sainburg (2002) suggested a modified access model, in which learned information through either one of the arms can be accessed and used by the other arm during subsequent task performance, based on its specialized control mechanism. The result of this study showed the increase of initial direction accuracy in the dominant arm and the increase in final position accuracy in the non-dominant arm after the opposite-arm training. In our experiment, task performance depended on how accurately the impact is made at the puck with the estimated direction and hand speed. Therefore, we expected, after the opposite arm training, the dominant arm will show better improvement in task performance than the non-dominant arm will do. Our hypothesis was not supported by the results, and we found contrasting results from our prediction: Subsequent task performance after opposite-arm training was similar in both arms.

This result may be due to the explicit information about the task from the initial training that could equally be accessed by both hemispheres. In the initial training with one arm, participants learned where to start the movement and how to strike the puck. It is possible that participants achieved the same level of task performance with the opposite arm by adopting the same strategy used with the previously trained arm. One perspective that might explain our result is from the study done by Malfait and Ostry (Malfait & Ostry, 2004), who suggested that the explicit awareness of the task dynamics can lead to interlimb transfer in the force-field adaptation learning. In their study, participants were asked to make a reaching movement with the right arm under two conditions. In one condition, the perturbation was introduced abruptly to the arm. In another condition, the perturbation was gradually introduced throughout the trials so that the participants could not consciously notice the force exerting on the arm. Then, interlimb transfer of learning was tested in the consequent trials with the left arm. The researchers hypothesized that the cognitive strategy information would be reduced by the gradual perturbation and this would impair the interlimb transfer. They found a significant effect of opposite-arm training in the abrupt condition; however, in the gradual condition, participants showed no effect of opposite-arm training. The researchers proposed that interlimb transfer might be involved with the use of information about the perturbation rather than the predictive control strategy developed by the initially trained arm. The same effect might have occurred in our current experiment. Both arms learned to maintain low task error by performing the task with the learned combination of the task variables at movement initiation and at puck impact. By planning the movement as they initially trained, participants might have shown the same extent of interlimb transfer in both directions.

Conclusions and limitations of the current study

In this study, we have asked several research questions related to motor lateralization and interlimb transfer on a skilled 2-D redundant shuffleboard task. The research questions include whether the dominant arm shows an advantage in learning a skilled task, how each arm exploits the redundancy embedded in the task, and how learning transfers to the arm from the initially training with the opposite arm. The purpose of the current study was to address motor lateralization questions on a skill-learning task. To do so, we created a 2-D redundant shuffleboard task that has the features of the skill-learning paradigm. Then, we asked participants to perform the task with either the dominant arm or the non-dominant arm during the two sessions on the first day. After 24 hours, they returned to practice one more session with the previous arm and another session with the opposite arm. On the first day, the dominant arm and the non-dominant arm showed a similar extent of reduction in task error with a similar time course.

We hypothesized that the dominant controller is specialized at predictive control of hand trajectory and task dynamics, so we predicted that the dominant arm will show better task learning and performance than the non-dominant arm. Our hypothesis was not supported by our results as both arms showed a similar extent of learning and a time course of learning. We suggest that this symmetrical task learning in both arms may be related to the similarity in the learned movement which may be performed with low intersegmental coordination. Similar results were reported in previous studies with a single elbow joint reaching movement and a multi-joint reaching movement (Sainburg & Kalakanis, 2000; Sainburg & Schaefer, 2004). We suggest that the effect of handedness is not prominently demonstrating on a planar skilled task when redundant degrees of freedom are allowed during the movement.

Moreover, we hypothesized that the CNS exploits the redundancy to maintain the skill level. This hypothesis was not supported by our results. After the task error was converged at the low level, participants in both groups didn't exploit the redundancy but rather utilized the local portion of redundancy. They initiate the movement at the upper center of the starting box and impact the puck with the least deviated angle and the optimum hand speed. This may be related to the optimization process that reduces control effort in the movement selection and execution, and this prevent participant exploit the redundancy. We suggest that exploitation of redundancy becomes limited when participants prioritize task performance on a planar skill task that has requirements to exploit the redundancy.

Lastly, we hypothesized that transfer of learning occurs in the limited form depends on the properties of the controllers. Our results didn't support this hypothesis as interlimb transfer of learning occurred in both directions on a task that predictive control plays a critical role for the task success. The symmetrical interlimb transfer of learning may be related to the utilization of the explicit learning of task strategy from the initial training. We suggest that the opposite arm driven information can be accessed by both controllers regardless of their specialized control mechanism.

One limitation of the current study is the shape of the starting box. In the 2-D shuffleboard task, we limited the participants' movement initiation location to be inside the rectangular box (Figure 9). The rectangular box might create bias when participants choose the movement initiation location, since the distance from the puck to the entire top border of the starting box is not consistent. One might choose not to initiate the strike from the left side or right side of the starting box because the distance to the puck is further; instead, one could easily take advantage of a shorter distance by choosing to initiate the movement from the center of the starting box. This bias interferes with our original purpose of allowing participants to initiate the task at their biomechanical preference. In future designs, the starting box should be in a semi-circular shape that has a consistent distance to the puck, to eliminate this bias.

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Appendix A

Edinburgh Handedness Inventory

Name: ______________________________

Address: ______________________________

____

Phone #: ____________________

Height: _________ **Weight:** ________ **Age:**________

Inclusion Information

Please check the appropriate boxes that pertain to you. It is not mandatory that you provide this information in order to participate in the study. The National Institutes of Health encourages tracking of gender and racial participation in research studies to ensure inclusion. As with all data that you provide for this study, the results are confidential.

Gender: Male [ ] Female [ ]

Ethnic Category	**Check**
Hispanic or Latino	
Not Hispanic or Latino	
I don't want to report this	
Racial Categories	
American Indian/ Alaska Native	
Asian	
Native Hawaiian or Other Pacific Islander	
Black or African American	
White	
More than one race	
I don't want to report this	

Handedness Questionnaire 1: Please check which hand you use for each task. If you use both hands, check both, bu indicate which one is used more often or that you feel is more controlled.

	R	**L**		**R**	**L**		**R**	**L**
Signing			Knife			Striking Match		
Writing			Spoon			Opening Box		
Drawing			Throwing			Foot to kick with		
Scissors			Broom (upper hand)			Bat (swing)		
Toothbrush								

1. Do you consider yourself: Right-Handed Left-Handed Ambidextrous (both hands)
2. Is there anyone in your family who is left handed? Yes or No If yes, then who:
3. Did you ever change handedness? Yes or No If yes, explain:
4. Is there any activity not in this list that you do consistently with your left hand? If so, please explain:

<u>Handedness Questionnaire 2:</u> This is a questionnaire to determine which side you use for manual activities. In the following questions, mark the letter [R] if you perform the certain activity with the right hand; [L] if you perform it with the left hand; and [E] if you can perform it easily with either hand. In all of these activities <u>consider your hands empty when</u> you begin to perform them.

	R	L	E
1. Which hand turns the knob in opening a door?			
2. Which hand throws a ball?			
3. With which hand do you hold a glass or cup, when drinking?			
4. Which hand holds a hammer when hammering			
5. Which hand holds the top when opening a jar?			
6. Which hand holds the scissors while cutting?			
7. Which hand pushes a light switch on the wall?			
8. Which hand distributes cards when dealing them?			
9. Which hand holds the tissue when blowing your nose?			
10. Which hand waves goodbye?			
11. Which hand tosses a coin?			
12. Which hand strikes a match?			
13. Which hand sets a watch?			
14. Which hand holds a toothbrush?			
15. Which hand takes money from your wallet or purse?			
16. Which hand holds a knife when cutting a loaf of bread?			
17. Which hand directs the thread through the eye of a needle?			
18. Which hand holds the spoon when stirring in a bowl?			
19. Which hand holds the comb or brush when you comb your hair?			
20. Which hand turns the pages in a book?			
21. Which hand holds the knife when peeling a potato?			
22. With which hand do you write?			
23. With which hand do you hold an eraser on paper?			
24. Which hand cuts with a knife when eating?			
25. Which hand uses a saltshaker?			
26. With which hand do you bounce a rubber ball?			
27. Which hand is on top when you applaud?			
28. With which hand do you draw a sketch or picture?			
29. Which hand turns the water faucet when you hold no glass in either hand?			
30. With which hand do you pick up a quarter from the floor?			
31. From which shoulder do you swing a bat?			
32. Which hand uses an eraser on a blackboard?			
33. Which hand is at the upper end of the handle when you shovel?			
34. Which hand holds a tennis racquet (badminton/racquetball/squash)?			
35. Which hand puts the key in a door keyhole?			

Do you consider yourself: Right-Handed Left-Handed Ambidextrous (both hands)

Is there any activity not in this list that you do consistently with your non-dominant hand, if so please explain:

Appendix B

The experiment checklist

Study Data Collection PREPARATION Form (Day 1)

IRB#: ______________ Subject I.D.: ______________ Date & Time: ______________

For completion PRIOR to the subject's arrival

For assessments:

Task:	**Instructions / Notes:**	**Complete?**	**Comments**
Paper materials are printed and set out	• Procedural checklist • Consent form • Demographics & Edinburgh's Handedness Inventory	☐ ☐ ☐	

With the system:

Task:	**Instructions / Notes:**	**Complete?**	**Comments**
System on and application loaded	Turn TrakStar, TV screen, speaker and Mac on	☐	
Kinereach software interface set-up	Does Kinereach read signals from the TrakStar? • Check if the coordinates are changing when you hit "run" button. Are checkboxes for the shuffleboard game selected as it is in the screenshot1? Are parameter values entered as it is in the screenshot? Targets and trials file were loaded correctly from the exact location? (Location: Desktop/JISUNG/P0055_ShuffleBoardTask/Experiment/Targets_Trials)	☐ ☐ ☐ ☐	
Create a new subject/session in Kinereach	Create a subject folder (with following template). • Template: Subject initial_ group_day (ex. JS_RL_1) (Location: Desktop/JISUNG/P0055_ShuffleBoardTask/Experiment/Subject)	☐	

In the lab:

Task:	**Instructions / Notes:**	**Complete?**	**Comments**
Kinereach equipment Set-up	**The sensors (4)** are connected to the TrakStar? **The transmitter** is connected to the TrakStar? **Air sled**☐, **arm stand**☐, **ties**☐ and **wrapping tapes**☐ are prepared on the table and ready to be used? Does Mac get signal from the wireless keyboard?	☐ ☐ ☐ ☐	
Tape is pre-torn	4 ~ 5 pieces	☐	

Other logistics:

Task:	**Instructions / Notes:**	**Complete?**	**Comments**
Compensation prepared; Parking pass	• Parking pass only if a subject indicated the need	☐	

Study Data Collection Form (Day 1)

IRB#: ______________________ Subject I.D.: ______________ Date: _______________

For completion AFTER the subject's arrival

1. **Preliminary Forms and Screening Assessments:**

Form:	**Instructions / Notes:**	**Complete?**	**Comments**
Consent Form & Handedness Inventory	Introduce forms to the participant and explain. • Consent form☐ • Demographics & Handedness Inventory ☐ Explain general procedures and experimental protocol. Mention that they will have a break in between the blocks. Have the participant read the forms and complete.	☐ ☐ ☐ ☐	
Verbal health history questions	1. Have you had any broken bones, surgery, or injury to upper extremities? 2. Do you have a history of neurological diseases likely to affect your ability to move upper extremities? 3. Do you have any significant problems with vision, hearing, or feeling in your hands/feet? 4. Do you play any sports or video games or musical instruments involved with upper extremity motion?	Y/N Y/N Y/N Y/N	Check for exclusion criteria (physical & neurological injuries, etc.)

2. **Digitization & Start:**

Form:	**Instructions / Notes:**	**Complete?**	**Comments**
Digitizing a subject	• Have participant sit comfortably while we digitize their upper extremity. • Digitize the subject in the following order.2 • Save the digitized coordinate file in the temporary folder. (Location: Desktop/JISUNG/P0055_ShuffleBoardTask/Experiment/Temporary)	☐ ☐ ☐	
Start the Shuffleboard game	• Click "Start" and load JPG from following location. (Location: Desktop/JISUNG/P0055_ShuffleBoardTask/Experiment/JPG Background) • Choose the subject folder you created to set as a data saving location.	☐ ☐	

3. **Instruction:**

Form:	**Instructions / Notes:**	**Complete?**	**Comments**
General introduction of Shuffleboard game & Scoring system	• Participant hit the puck to the rainbow target with the cursor.	☐	
	• The participant can aim at any location in the rainbow target.	☐	
	• The participant should start reaching move inside of the box.	☐	
	• Black, red, and a blue color band give 10, 3, and 1 point respectively.	☐	
	• Instruct participants to not use trunk while performing the task.	☐	

4. **Shuffleboard Trials:** ****MAKE KINEREACH FILE NAMES TRIAL-SPECIFIC****

Day 1	
Block 1 (300 trials)	☐
Break (1 min~5 min)	☐
Block 2 (300 trials)	☐

Check Kinereach to ensure data files for all conditions and trials!
END DATA COLLECTION

Following Data Collection:

	Complete?
Remove sensors and tapes:	☐
Compensate participant for day 1 ($10):	☐
Adjust Kinereach data according to initial of the participant and arm. **(ex. JS1 and JS2 depends on the arm)**	☐
Move data files to the external hard drive	☐

Notes:

Study Data Collection PREPARATION Form (Day 2)

IRB#: ______________________ Subject I.D.: ______________ Date & Time: _______________

For completion PRIOR to the subject's arrival

With the system:

Task:	**Instructions / Notes:**	**Complete?**	**Comments**
System on and application loaded	Turn TrakStar, TV screen, speaker and Mac on	☐	
Kinereach software interface set-up	Does Kinereach read signals from the TrakStar? • Check if the coordinates are changing when you hit "fly" button. Are checkboxes for the shuffleboard game selected as it is in the screenshot1? Are parameter values entered as it is in the screenshot? Targets and trials file were loaded correctly from the exact location? (Location: Desktop/JISUNG/P0055_ShuffleBoardTask/Experiment/Targets_Trials)	☐ ☐ ☐ ☐	
Create a new subject/session in Kinereach	Create a subject folder (with following template). • Template: Subject initial_ group_day (ex. JS_RL_1) (Location: Desktop/JISUNG/P0055_ShuffleBoardTask/Experiment/Subject)	☐	

In the lab:

Task:	**Instructions / Notes:**	**Complete?**	**Comments**
Kinereach equipment Set-up	**The sensors (4)** are connected to the TrakStar? **The transmitter** is connected to the TrakStar? **Air sled**☐, **arm stand**☐, **ties**☐ and **wrapping tapes**☐ are prepared on the table and ready to be used? Does Mac get signal from the wireless keyboard?	☐ ☐ ☐ ☐	
Tape is pre-torn	4 ~ 5 pieces	☐	

Other logistics:

Task:	**Instructions / Notes:**	**Complete?**	**Comments**
Compensation prepared; Parking pass	• Parking pass only if a subject indicated the need	☐	

Study Data Collection Form (Day 2)

IRB#: ______________ Subject I.D.: ______________ Date: _______________

For completion AFTER the subject's arrival

1. **Re-cap from day 1:**

Form:	Instructions / Notes:	Complete?	Comments
Remind participants about the general rules	Explain general procedures and experimental protocol. Mention that they will have a break in between the blocks.	☐ ☐	

2. **Digitization & Start:**

Form:	Instructions / Notes:	Complete?	Comments
Digitizing a subject	• Have participant sit comfortably while we digitize their upper extremity. • Digitize the subject in the following order.2 • Save the digitized coordinate file in the temporary folder. (Location: Desktop/JISUNG/P0055_ShuffleBoardTask/Experiment/Temporary)	☐ ☐ ☐	
Start the Shuffleboard game	• Click "Start" and load JPG from following location. (Location: Desktop/JISUNG/P0055_ShuffleBoardTask/Experiment/JPG Background) • Choose the subject folder you created to set as a data saving location.	☐ ☐	

3. **Instruction:**

Form:	Instructions / Notes:	Complete?	Comments
General introduction of Shuffleboard game & Scoring system	• Participant hit the puck to the rainbow target with the cursor. • The participant can aim at any location in the rainbow target. • The participant should start reaching move inside of the box. • Black, red, and a blue color band give 10, 3, and 1 point respectively. • Instruct participants to not use trunk while performing the task.	☐ ☐ ☐ ☐ ☐	

4. Shuffleboard Trials: ****MAKE KINEREACH FILE NAMES TRIAL-SPECIFIC****

Day 2	
Block 1 (300 trials)	☐
Break (1 min~5 min)	☐
Block 2 with the opposite arm (300 trials)	☐

Check Kinereach to ensure data files for all conditions and trials!
END DATA COLLECTION

Following Data Collection:

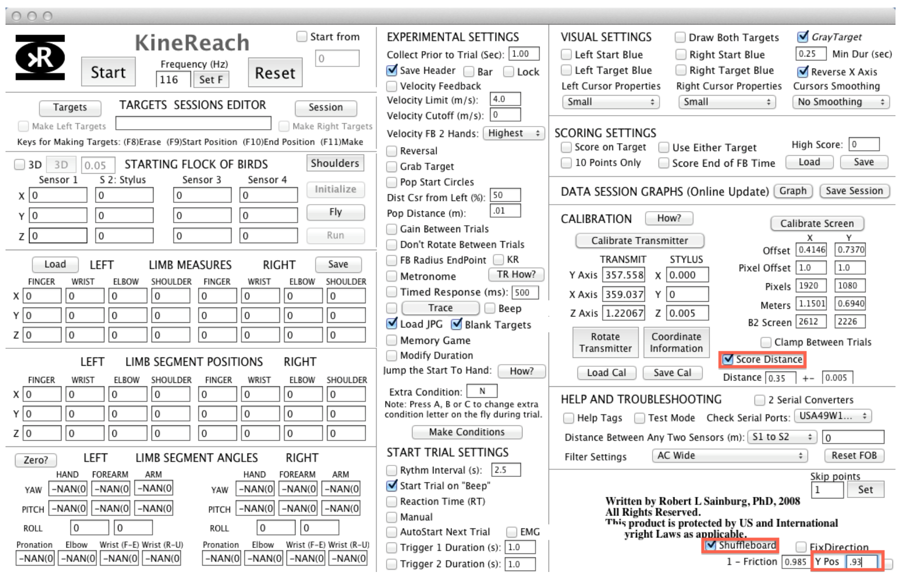
	Complete?
Remove sensors and tapes **Compensate participant for day 1 ($20)**	☐ ☐
Adjust Kinereach data according to initial of the participant and arm. **(ex. JS1 and JS2 depends on the arm)**	☐
Move data files to the external hard drive	☐

Notes:

Appendix C

Kinereach set-up and digitazation procedure

1. Kinereach set-up screenshot



2. Digitization procedure

1. Use the **right-hand** sensor to digitize the subject.
    a. Note: you will need either a wireless keyboard or a helper during this.
2. Always start with the right arm.
3. Use keyboard keys F1-F7 to digitize the right side
4. Use keyboard keys 1-7 to digitize the left side
5. Digitize in this order:
    a. Between proximal phalanx and middle phalanx of index finger
    b. Between MCP joint of ring and middle finger
    c. Distal end of the radius (medial when subject wrist is prone)
    d. Distal end of ulna (lateral when subject wrist is prone)
    e. Medial epicondyle of humerus
    f. Lateral epicondyle of humerus
    g. Acromion process
6. Then, tape the sensor to the insertion of the middle deltoid
7. Press 8
8. Next, check your digitization by comparing the Kinereach's calculated elbow angles to subject's actual angles (ex. Put subject's arm in 90 degrees)
9. Save these measurements by clicking *Save* under Limb Measurements just in case the Kinereach crashes.

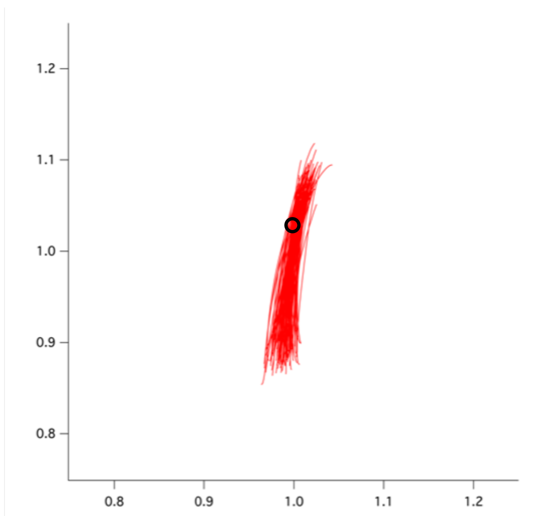
Appendix D

Individual hand trajectories for both groups in trial 200 ~ 300 of session 2.

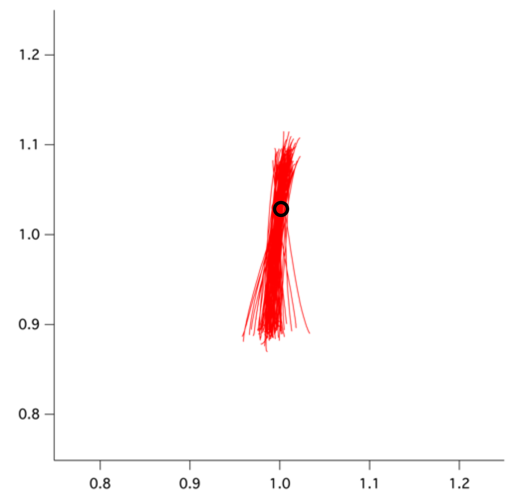
The black empty dot indicates the initial position of the puck's center. The red line indicates the hand trajectory, and these hand trajectories are made during 200th ~ 300th trials in session 2.

RL group

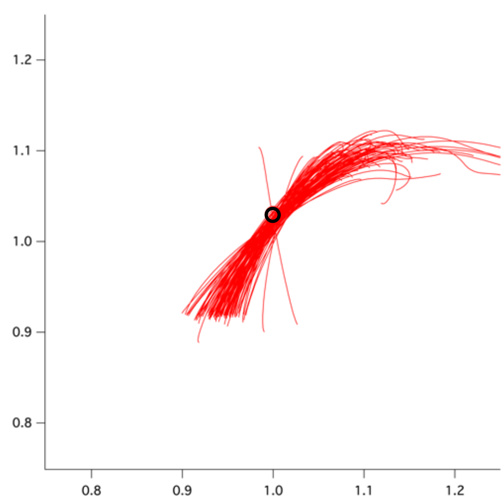
Participant 1



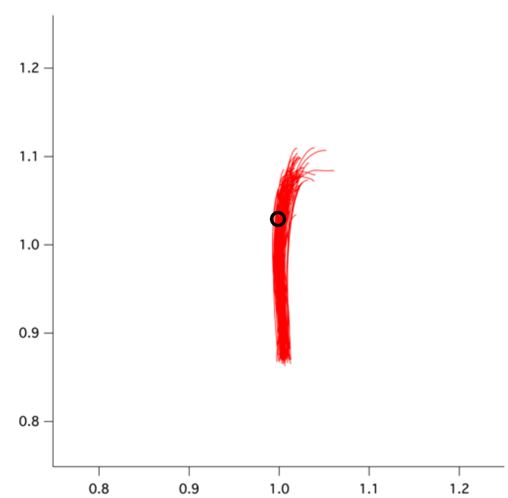
Participant 2



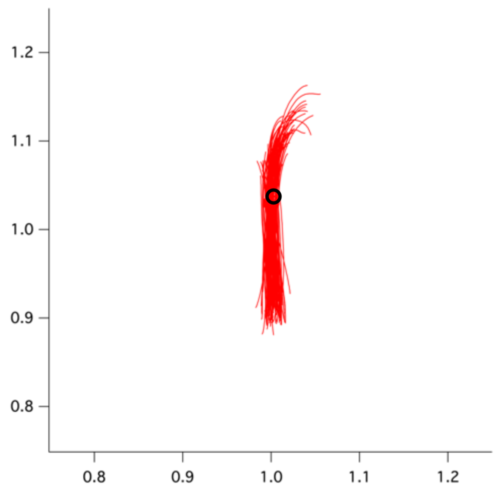
Participant 3



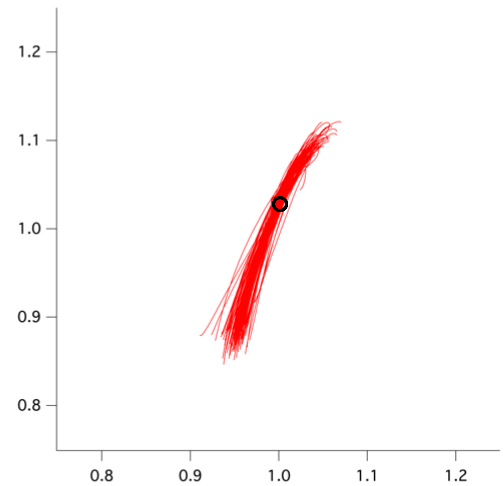
Participant 4



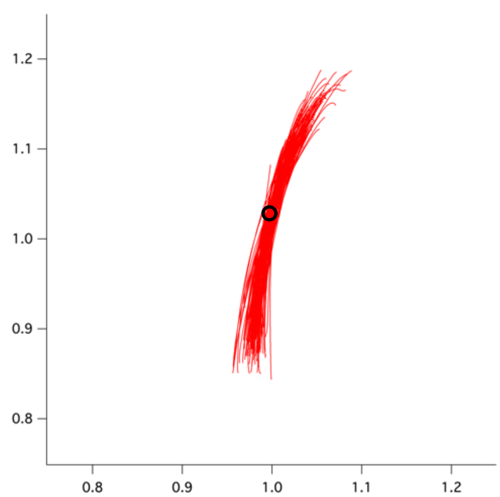
Participant 5



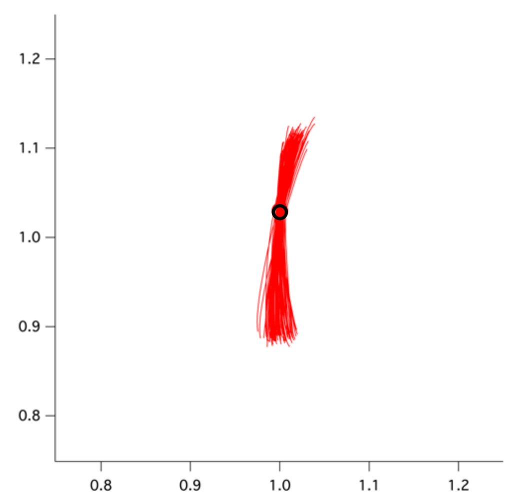
Participant 6



Participant 7

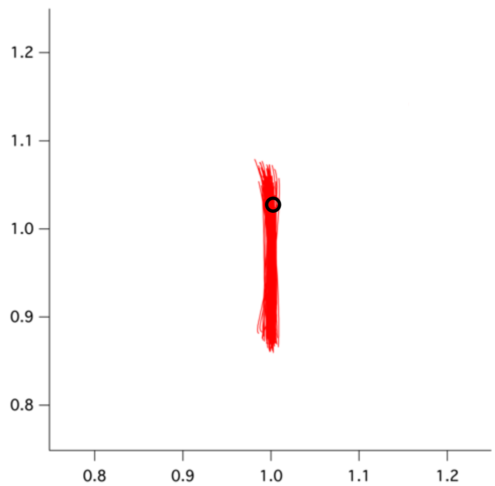


Participant 8

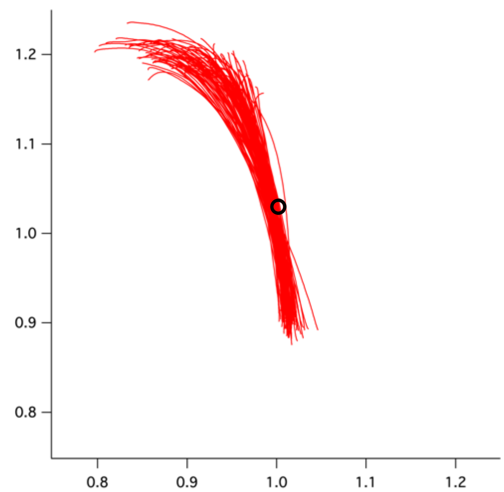


LR group

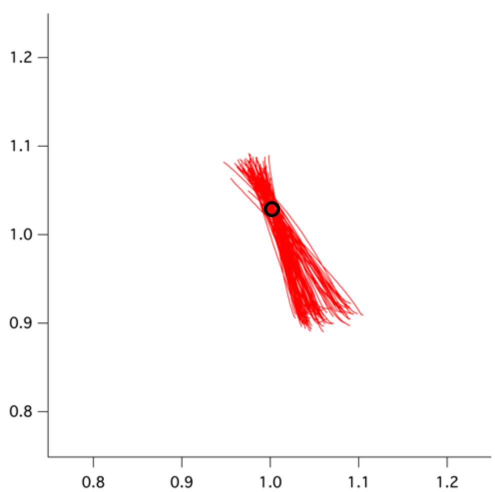
Participant 1



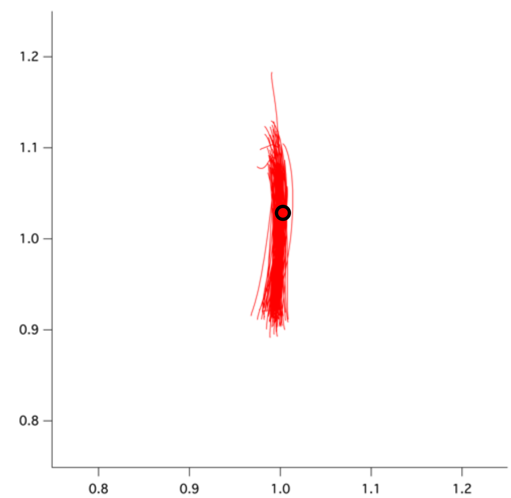
Participant 2



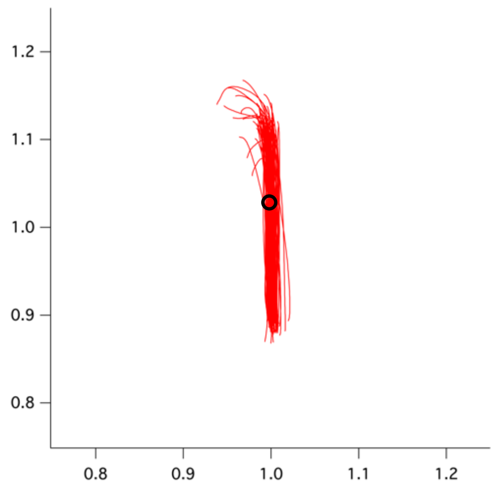
Participant 3



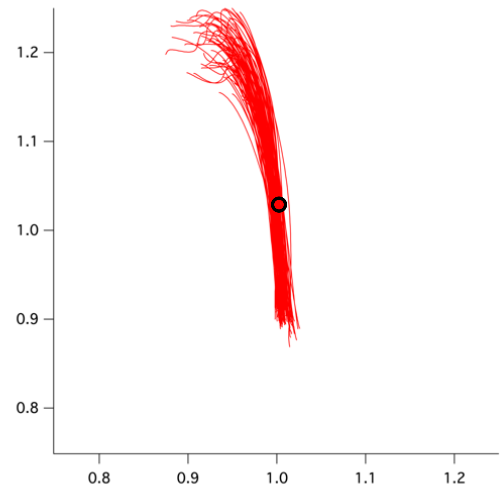
Participant 4



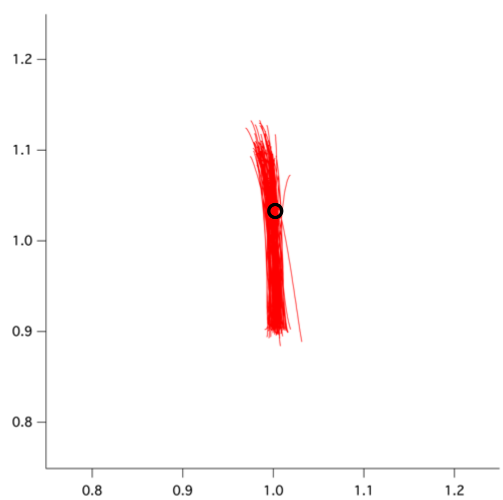
Participant 5



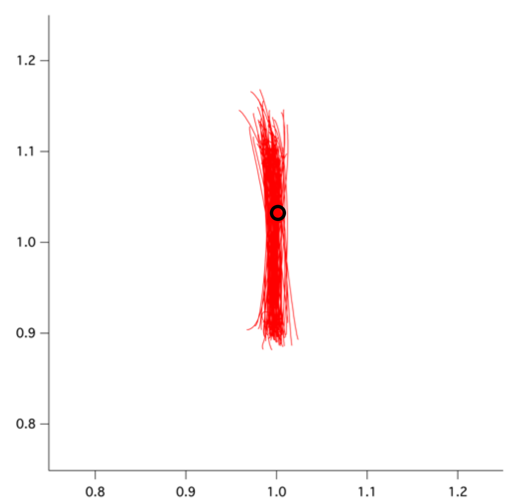
Participant 6



Participant 7



Participant 8



Appendix E

The participants' demographics

LR Group				
Participant	**Sex**	**Age**	**Height(cm)**	**Weight(kg)**
aa	M	23	180.4	76
bb	M	24	177.8	82
cc	M	22	185.4	84
dd	M	26	175.3	73
	Mean	23.75	179.73	78.75
	Stdev	1.71	4.32	5.12
ee	F	27	154	50
ff	F	21	170.2	84
gg	F	29	165.1	51
hh	F	28	170	55
	Mean	26.25	164.83	60.00
	Stdev	3.59	7.59	16.15

RL Group				
Participant	**Sex**	**Age**	**Height(cm)**	**Weight(kg)**
ii	M	26	172.7	64
jj	M	24	177.8	64
kk	M	23	180.4	68
ll	M	24	186	81
	Mean	24.25	179.225	69.25
	Stdev	1.26	5.53	8.06
mm	F	30	160	47
nn	F	23	162	58
oo	F	18	160	52
pp	F	28	160	47
	Mean	24.75	160.50	51.00
	Stdev	5.38	1	5.23