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INVESTIGATING THE CONTRIBUTION OF INSTANCE-RELIANT LEARNING IN VISUOMOTOR ADAPTATION AND ITS GENERALIZATION

by

Shancheng Bao

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ABSTRACT

INVESTIGATING THE CONTRIBUTION OF INSTANCE-RELIANT LEARNING TO VISUOMOTOR ADAPTATION AND ITS GENERALIZATION

by

Shancheng Bao

The University of Wisconsin-Milwaukee, 2019
Under the Supervision of Professor Jinsung Wang

Motor adaptation has been of great interest in the past two decades as it reflects how movement skills are acquired and consolidated by the nervous system. In our recent studies, instance-reliant learning is considered as an essential component of visuomotor adaptation, since it plays a unique role in fast and automatized control of movement output. The goal of this dissertation is to investigate the nature of instance-reliant learning on two aspects: to determine the differential contributions of algorithmic learning and instance-reliant learning to visuomotor adaptation; and to determine the nature of movement instance involved in visuomotor adaptation and its generalization across different situations that involve magnitude, workspace, and limb configuration. Experimental results show that both algorithmic and instance-reliant learnings are positively associated with the improvements in the subsequent performance, which is compatible with our expectation. However, compared to algorithmic learning, which has been intensively studied before, instance-reliant learning exhibits different characteristics in terms of both visuomotor adaptation and its generalization. In Experiment 1 and 2, we found that algorithmic and instance-reliant learning led to substantial improvements in movement errors; but the learning rate in the subsequent test was only sensitive to algorithmic learning. In Experiment 3, 4, and 5, the movement instances associated with the reaching performance were magnitude, workspace, and limb configuration specific, although it could still generalize to a certain degree. Thus, the distinct contributions of instance-reliant learning to motor adaptation are elucidated in this dissertation. We expect that findings from this dissertation would prove valuable for developing rehabilitation strategies for patients who suffer from neuromotor impairments.

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CHAPTER 1: Introduction

Adaptation is a particular form of motor learning in which the central nervous system (CNS) minimizes the movement errors that are introduced by altered external perturbations (Wang & Sainburg 2003, 2004; Krakauer et al., 2005; Krakauer 2009; Buch et al., 2009). In a typical laboratory set up, the participants are required to make a center-out reaching movement towards a target, while an environmental perturbation is imposed through a virtual reality environment (Wang & Sainburg 2003, 2004; Krakauer et al., 2005; McDougle et al., 2015), an external force-field (Shadmehr & Mussa-Ivaldi, 1994; Miall & Wolpert, 1996; Kawato, 1999; Smith, et al., 2006), or a prism goggle (Gaveau, et al., 2014; Block & Bastian, 2012). In regular learning, e.g., vehicle driving or keyboard playing, the formation of new spatiotemporal patterns usually takes several days or weeks (Sanes, 2000; Shadmehr & Moussavi, 2005); in motor adaptation, in contrast, the CNS only needs to adjust the controlling policy for one single context to adapt to the systematic perturbation, so it usually takes only a few minutes to reduce the sensory feedback error to the baseline level (Sanes, 2000; Shadmehr & Moussavi, 2005; Wang & Sainburg, 2003, 2004; Krakauer et al., 2005; Krakauer, 2009; Buch et al., 2009). Thus, in the past twenty years, adaptation has been frequently applied as a simplified paradigm to investigate the nature of motor control/learning. In this dissertation, we focus on two learning mechanisms: algorithmic learning and instance-reliant learning. We will examine their relative contributions to visuomotor adaptation separately (Chapter 2) and will investigate the nature of movement-specific instances during the active and passive movement training (Chapter 3 and 4).

Algorithmic learning in motor adaptation

The adaptation to the systematic perturbation is considered to involve an internal model in which the CNS recalibrates the visual-motor map to minimize the sensory feedback error. In the literature, this mechanism is termed model-based learning (Cunningham, 1989; Kawato, 1999; Donchin, et al., 2003; Shadmehr & Wise, 2005; Huang et al., 2011), error-based learning (Seidler, 2013; Diedrichsen et al., 2010), or algorithmic learning (Wang & Sainburg, 2004; Wang et al., 2015; Lei et al., 2017; Bao et al., 2017). In this dissertation, we use the term algorithmic learning to be consistent with our previous publications (Wang & Sainburg, 2004; Wang et al., 2015; Lei et al., 2016, 2017; Bao et al., 2017). The procedure to adjust the visuomotor map can be mimicked by a state-space model as shown below (Thoroughman & Shadmehr, 2000; Francis & Wonham, 1976; Baddeley et al., 2003; Donchin et al., 2003):

$$x[n + 1] = a*x[n] + b*u[n] \qquad (1)$$

$$y[n] = x[n] + d*u[n] \qquad (2)$$

Here x represents the current state of the internal model, y represents the output of the motor system, n is the index of task trials, a is the retention factor of the system, b is the learning rate which quantifies the sensitivity to experienced errors, and u indicates the sensory feedback error. This model suggests that the internal state is adjusted in a step by step manner based on the current state $x[n]$ and the sensory feedback error $u[n]$. The efficiency of this system is determined by the two constants a and b.

The cerebellum is considered the key neural substrate involved in the error-based calibration (Criscimagna-Hemminger et al., 2010; Ramnani, 2006; Tseng et al., 2007; Mazzoni et al., 2006; Seidler, 2013), as it plays a crucial role in error detection and correction in motor performance. For example, in daily reaching/tracing movement, the activation of the cerebellum increases largely when we attempt to correct the movement errors through visual feedback, and the increased activation returns to baseline level when we stop correcting the errors (Ogawa et al., 2006). People with cerebellar lesions might exhibit normal performance in reaching movements; however, compared to neurologically intact people, they are less able to adapt to either the force field (Smith & Shadmehr, 2005; Criscimagna-Hemminger et al., 2010) or the visuomotor rotation (Tseng et al., 2007; Taylor et al., 2010; Hashimoto et al., 2015; Synofzik et al., 2008).

Instance-reliant learning in motor adaptation and its generalization

Instance-reliant learning, also known as use-dependent learning/plasticity (Wang & Sainburg, 2004; Wang et al., 2015; Lei et al., 2016, 2017; Bao et al., 2017; Diedrichsen et al., 2010), is defined as the process in which movement-specific instances are accrued and retrieved automatically later to allow fast and automatized control of the task. Due to the plasticity of the brain, intensive practice of the same movement results in functional and structural reorganization (Butefisch et al., 2000; Ganguly & Poo, 2013; Pascual-Leona et al., 1995; Liepert et al., 1999), and this kind of reorganization usually leads to changes in subsequent performance (Classen et al., 1998; Diedrichsen et al., 2010; Pascual-Leona et al., 1995). For example, Classen (1998) compared the transcranial magnetic stimulation (TMS) elicited thumb movements before and after the training. He found that after 15 minutes of thumb flexion/extension training in a fixed direction, the same TMS evoked an altered movement which biased towards the trained direction. This phenomenon shows that neural pathways that encode the kinematic details were adjusted, so the corticomuscular coherence is not the same after the 15 minutes training. The reorganization within the cortex is observable and stable in the long term. In another study, Pasual-Leone (1995) investigated the effect of training on corticomuscular coherence. He had the subject practice hand/finger exercise on a piano for five days and mapped the cortical areas targeting the finger muscles through TMS, finding that the finger areas enlarged and the motor threshold decreased.

The contribution of instance-reliant learning to motor adaptation has been proved by examining the transfer of adaptation across limbs (Wang & Sainburg, 2004; Wang et al., 2015; Lei et al., 2017; Bao et al., 2017). In the literature, the extent of interlimb transfer is typically limited to about 30% (Carroll et al., 2014; Taylor et al., 2014; Wang & Sainburg, 2003, 2004; Lei & Wang, 2014). The fact that interlimb transfer occurs suggests that the left and right limbs share some neural processes (Wang & Sainburg, 2003, 2004); and the fact that the extent of interlimb transfer is limited suggests that each limb has only partial access to the information obtained during motor adaptation with the opposite limb. In our previous studies, we posited that instance-reliant learning was effector-specific, so training on one arm did not reorganize the corresponding neural pathways for the opposite arm (Wang et al., 2015; Lei et al., 2017; Bao et al., 2017), and the achieved adaptation by one arm could hardly benefit the performance of the other arm. To test this idea, Wang (2015) had the subjects accrue instances associated with the task by both arms, but learn the task with only the left arm. After that, the authors tested the performance of the subjects' right arm, finding that the transfer increased to be above 80%. Since the instances were provided to the right arm without adaptation, the changes in interlimb transfer could only be attributed to instance-reliant learning.

Use-dependent plasticity and stroke rehabilitation with robotics

One of the most important clinical applications of instance-reliant learning is the rehabilitation intervention for stroke patients (Kent et al., 2009; Kreisel et al., 2006; Nudo et al., 2001). After the stroke attack, novel pathways are created to compensate for the lost networks within the lesion (Kreisel et al., 2006; Nudo et al., 2001; Kent et al., 2009). Many endogenous and exogenous events can trigger the modulation of cortical/subcortical substrates, while the behavioral experience is considered as one of the most potent factors (Nudo et al., 1996, 2013; Karni et al., 1998; Gerloff et al., 2006; Lotz et al., 2006).

Physical exercise is important to maximize the effect of neuroplasticity after stroke (Butefisch et al., 2000; Chang & Kim, 2013). Even in the chronic stage, high-dose intensive training and repetitive practice of specific functional tasks could still lead to neural reorganization (Sawaki et al., 2006; Kent et al., 2009; Dancause, 2006; Kreisel et al., 2007; Butefisch et al., 2000; Nudo et al., 2001; Wittenberg et al., 2003) and motor improvement (Wolf et al., 2006; Sawaki et al., 2014; Liepert et al., 1998; Taub et al., 1999). For example, Wolf (2006) reported that patients who received a 2-week program of constraint-induced movement training showed substantial improvement in arm motor function, and the effect of this training persisted for a long term (> 1 year). In a similar study, Sawaki (2014) showed the same result as Wolf, and he found that the patients who received the treatment in the early stage (< 9 months post-stroke) exhibited even more improvement in motor function than those who received the treatment in the late stage.

In the past twenty years, robotic-assisted therapy has developed remarkably with powerful embedded programs and sophisticated mechanical components. Compared to the traditional hand-to-hand therapy approach, robotic-assisted therapy shows advantages in two aspects. First, it is more effective in delivering higher-intensity and high-dosage training, which would maximize the effect of use-dependent reorganization (Hesse et al., 2003; Kwakkel et al., 1999; Hsieh et al., 2012). Second, it enables the patients to undergo active assistive exercises through wearable devices, which could trigger recoveries for specific movement tasks. A large number of studies have shown that the effect of robotic therapy is no worse or better than the traditional hand-to-hand approach (Chang & Kim, 2013; Hesse et al., 2003; Aisen et al., 1997). For example, Chang (2013) reviewed 38 studies that compared the effects of robotic-assisted therapies and traditional therapies. In more than half of the studies, robotic-assisted therapies led to better recoveries; in only two studies, the patients achieved better recoveries with the traditional therapies (Hornby et al., 2008; Hidler et al., 2009). This result suggests that robotic therapy might play more critical roles in stroke rehabilitation in the future.

Summary

In this chapter, we reviewed the mechanisms of algorithmic learning and instance-reliant learning. As discussed above, a better understanding of these two processes, especially the latter one, not only has potential for coaching methodology and rehabilitation but also provides insights into the structural and functional reorganizations in cortical regions. In this dissertation, the purpose is to investigate the nature of instance-reliant learning in two aspects: comparing the relative contributions of algorithmic learning and instance-reliant learning to the formation of a neural representation associated with visuomotor adaptation; investigating the nature of movement specific instances in visuomotor adaptation and its generalization. We expect that findings from this study will prove valuable for developing novel rehabilitation interventions for optimal motor/sensory recoveries in the future.

Statement of Purpose

The purpose of this dissertation is twofold. As described below, in the first session, we estimate the contribution of algorithmic and instance-reliant learning to visuomotor adaptation. In the second session, we investigate the nature of movement instance in three aspects.

Aim I: To determine differential contributions of algorithmic and instance-reliant learning to visuomotor adaptation. This specific aim has two sub-aims, as shown below:

Aim Ia: To examine the effects of varying degrees of algorithmic learning on visuomotor adaptation.

Working hypothesis: If algorithmic learning plays a critical role in visuomotor adaptation, the extent of adaptation will vary as a function of the degree of algorithmic learning.

Aim Ib: To examine the effects of varying degrees of instance-reliant leaning on visuomotor adaptation.

Working hypothesis: If instance-reliant learning plays a critical role in visuomotor adaptation, the extent of adaptation will vary as a function of the degree of instance-reliant learning.

Aim II: To determine the nature of direction-specific instances involved in visuomotor adaptation and its generalization. This specific aim has three sub-aims, as shown below:

Aim IIa: To examine the patterns of generalization following visuomotor adaptation across movement conditions in which the direction of motor instances remains the same, but the amplitude of motor instances varies.

Working hypothesis: if instance-reliant learning depends on movement amplitude, the patterns of generalization following visuomotor adaptation will vary across movement conditions in which the amplitude of movement instances varies.

Aim IIb: To examine the patterns of generalization following visuomotor adaptation across movement conditions in which the direction of the motor instances remains the same, but the workspace of motor instances varies.

Working hypothesis: If instance-reliant learning depends on workspace locations, the patterns of generalization following visuomotor adaptation will vary across movement conditions in which the workspace of motor instances varies.

Aim IIc: To examine the patterns of generalization following visuomotor adaptation across movement conditions in which the direction of motor instances remains the same, but the limb configuration varies.

Working hypothesis: If instance-reliant learning depends on joint configurations, the patterns of generalization following visuomotor adaptation will vary across movement conditions in which the limb configuration varies.

The remainder of this dissertation is outlined as follows: Chapter 2 describes Experiments 1 and 2 that are conducted to achieve Aims Ia and Ib, respectively. Chapter 3 describes Experiment 3 that is conducted to achieve Aim IIa. Chapter 4 describes Experiments 4 and 5 that are conducted to achieve Aim IIb and IIc, respectively. Finally, Chapter 5 describes the summaries and conclusions.

Delimitations of the Study

1. The studies are designed based on an idea that algorithmic and instance-reliant learning constitute the visuomotor adaptation.
2. Data are collected on healthy young adults. Thus, any generalizations of the findings in this study will be limited to such a population.

3. We investigate algorithmic and instance-reliant learning through observational learning and passive movement training. Therefore, findings from the present study should be generalized to other types of learning with caution.

Assumptions of the Study

1. Participants do not have any neurological disorder.
2. Participants honestly follow all instructions regarding the experimental procedures.

Significance of the Study

The idea of instance-reliant learning has been presented and discussed in previous publications. That is, it was used to explain the findings from studies that investigated the interlimb transfer of visuomotor adaptation (Wang & Sainburg, 2003; 2004; Wang et al., 2015; Lei et al., 2014, 2016, 2017; Bao et al., 2017). However, the nature of the movement specific instances in motor control remains to be further investigated. This study is of theoretical importance, as it provides further insights into the mechanisms of algorithmic and instance-reliant learning. Moreover, it is also of practical importance, in that the findings from this study may prove valuable for developing optimal rehabilitation interventions for clinical populations (e.g., stroke survivors with severe hemiparesis).

CHAPTER 2: Contributions of Algorithmic Learning and Instance-Reliant Learning to Visuomotor Adaptation

In Chapter 1, we have introduced two main learning processes in motor adaptation: instance-reliant learning and algorithmic learning. In this study, in order to estimate the differential contributions of algorithmic and instance-reliant learning to visuomotor adaptation, we replace the active movement training with a combination of observation and passive movement training. In this way, we are able to investigate these two types of learning separately.

Introduction

Motor skills are usually acquired through intensive physical practice; however, by observing another individual undergoing the process of learning, motor learning can also be accomplished or partially achieved (Brass et al., 2000, 2001; Black & Wright, 2000; Heyes & Foster, 2002; Hayes et al., 2010; Kelly et al., 2003; Lei et al., 2016; Mattar & Gribble, 2005; Hodges et al., 2007; Moisello et al., 2009; Vogt, 1995). The effects of movement observation on choice response time tasks (Brass et al., 2000, 2001), and serial reaction time tasks (Moisello et al., 2009; Heyes & Foster, 2002; Hayes et al., 2010) have been examined in a large number of studies, and almost all of them show that the learning effects are substantial and robust (Black & Wright, 2000; Mattar & Gribble, 2005; Moisello et al., 2009; Ong & Hodges, 2010; Kelly et al., 2003).

During visuomotor adaptation, the updating of visuomotor maps is usually accomplished through repetitive and active practice of the movement task (Conchin & Martineau, 2003; Shadmehr & Wise, 2005; Kawato, 1999); however, recent studies indicate that this process could be partially achieved through movement observation, too (Mattar & Gribble, 2005; Lei et al., 2016; Ong & Hodges, 2010). For example, Mattar (2005) had the subjects observe a model who learned to reach towards a target in a force field, finding that the subjects showed improved performance if they were provided with the same force field that they had observed. Mattar posited that observation led to implicit movement planning in his study, so the subjects were able to learn how to compensate for the external perturbation even though they had not actively practiced the movement task themselves. A recent study in our lab had also investigated the effects of movement observation (Lei et al., 2016). We got similar results that observation tasks substantially reduced the direction errors in a reaching task when the visual display was distorted, confirming that visuomotor adaptation can also be achieved through movement observation.

Movement observation could provide explicit knowledge about the systematic perturbation (Ong & Hodges, 2010). Thus, it is possible that subjects intentionally adjust their directions through strategic implementations (Mazzoni & Krakauer, 2006; Benson et al., 2011; Taylor et al., 2014, 2015). However, the influence of the explicit process seems to be limited to an acceptable range for two reasons. First, a large number of the subjects are unaware of the perturbation after the observation (Mattar & Gribble, 2005; Ong & Hodges, 2010; Lei et al., 2014), indicating that we cannot merely attribute the improvements in performance to the explicit knowledge. Second, the action of observation demands little attention (Marquez & Wenderoth, 2011), so the subjects tend to pay limited cognitive effort to the observed tasks. For example, in Mattar’s study, he had the subjects perform an arithmetic task during the observation, yet this secondary task had no influence on the learning effects at all, indicating that the observation did not cost too much effort, and the subjects were less likely to think about a strategy to intentionally bias their movement directions.

Based on the introduction above, we conclude that algorithmic learning can be induced by having the subject observe a video that another individual learn to adapt to the visuomotor rotation. Explicit knowledge might be inevitable, but it can be restricted to an acceptable range (Mattar & Gribble, 2005; Ong & Hodges, 2010). Instance-reliant learning is also inhibited during the observation as the observer does not perform the reaching task.

Instance-reliant learning is another important process in the visuomotor adaptation as we have described in Chapter 1 (Wang & Sainburg, 2003, 2004; Wang et al., 2015; Lei et al., 2017; Bao et al., 2017). One way to accrue movement specific instances is to have the subject passively repeat the movement which is guided by a robotic system (Diedrichsen et al., 2010; Sakamoto et al., 2015; Lei et al., 2016, 2017; Bao et al., 2017). Since the movement instance is passively acquired, direction errors are not delivered to the CNS through visual feedback, so that algorithmic learning is inhibited during the passive movement training.

In order to manipulate the degrees of algorithmic learning and instance-reliant learning in visuomotor adaptation, the active reaching movement was replaced by two separated tasks in this study: (a) algorithmic learning, which was induced through movement observation; and (b) instance-reliant learning, which was induced through passive movement training. To achieve Aim 1a, we manipulated the number of observation trials, but kept the passive trials unchanged in Experiment 1; and for Aim 1b, we manipulated the number of passive trials, but kept the observation trials unchanged in Experiment 2. We hypothesized that varying degrees of algorithmic learning and instance-reliant learning would influence the extent of visuomotor adaptation.

Experiment 1

The purpose of Examine 1 was to investigate the effects of varying degrees of algorithmic learning on the extent of visuomotor adaptation.

Materials and Methods

Participants

A total of thirty-two neurologically intact right-handed individuals (19 males and 13 females) participated in this study. Informed consent was solicited from each subject before the participation, using a form approved by the Institutional Review Board of the University of Wisconsin-Milwaukee (Appendix A). Handedness was assessed using the Edinburgh Handedness Inventory (Appendix B; Oldfield, 1971). The participants were recruited on the campus of University of Wisconsin Milwaukee through word of mouth or posted flyers (Appendix C). Inclusion criteria were: (a) the subject fell in the age range 18-35; (b) no neurological disease or peripheral disorder affected the movement of the limbs. Exclusion criteria after the data collection were: (a) the subject was unable to complete assessment due to a low level of consciousness, developmental delay, low literacy, or inability to use English; (b) the subject had a neurological disease or peripheral disorder affecting movement of the upper limbs; (c) the subject had a vision impairment including color-blindness. According to our previous studies, the sample size of thirty-two subjects (four groups, eight per group) was large enough to meet the most stringent statistical requirement.

Apparatus

The BKIN Dexterit-E^{TM} system (BKIN Technologies Ltd, Kingston, ON, Canada) is a robotic system, which is usually used for tracking the performance of upper limbs in behavioral studies (Figure 2.1). This system consists of two KINARM Exoskeleton robots, a 2D virtual reality display, Dexterit-E^{TM} experimental control and data acquisition system. The position and length of the two robots can be adjusted to fit the individual's size and allow for full specification of limb configuration. The 2D virtual reality display is used to present visual stimuli in such a way that the projected vision appears at the same horizontal level as the hand. Dexterit-E^{TM} experimental control and data acquisition software are designed to run on a multi-computer system which acts as an interface for choosing task protocols, providing visual feedback to the operator, and saving the experimental data.

The recruited subject was seated in the KINARM chair with the arms supported by exoskeletons that provided full gravitational support of the arm. Direct vision of the arm was blocked, and a cursor representing the position of the index finger was displayed on the screen to guide the reaching movements. 2D hand-position data were sampled at 1000 Hz, low-pass filtered at 15 Hz, and differentiated to yield resultant velocity and position values. The output data were processed using Matlab (Mathworks, Natick, MA).

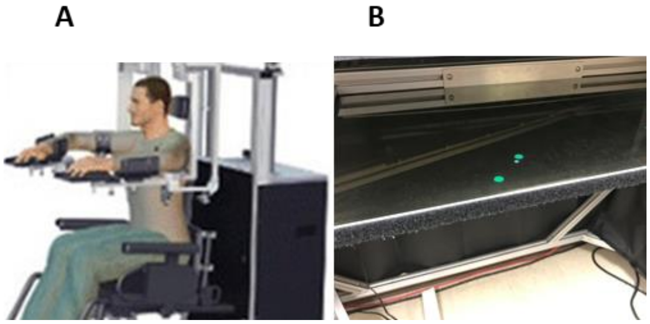

Figure 2.1: BKIN Dexterit-E System. A. Experimental setup for the subject (from Mostafavi et al., 2015). The movements of the arms are restricted and monitored by the exoskeleton within a horizontal plane. B. Virtual display of visual stimulus for a reaching task.

Experimental Protocol

During the active reaching performance, subjects repeatedly performed reaching movements through a cursor indicating the location of the right index fingertip from a start circle to a target (both 2 cm in diameter) which was 10 cm away from the start circle. They were instructed to reach rapidly and as straight as possible towards one of four targets in response to a "go" signal. The experiment consisted of three sessions: baseline, training, and testing. The baseline session contained 15 cycles (60 trials) of reaching movement and each cycle comprised four consecutive trials corresponding to the four targets, which were placed on directions of 45^o, 135^o, 225^o, and 315^o (Figure 2.2A). Veridical position of the index fingertip was provided to the subjects by a cursor displayed on the screen, so the subjects became familiar with the general reaching task.

The training session consisted of 8 blocks of movements, as shown in Figure 2.2C. Each block contained a number of observation trials (the number varied across conditions; see below) in which the subjects observed a video of a naïve model who performed a reaching movement under the visuomotor rotation condition, along with 20 trials of passive reaching movements. The visuomotor rotation was shown in Figure 2.2B. The display of the cursor was 30^o counterclockwise to the position of the right index finger (i.e., hand movement made in the 12 o'clock direction results in cursor movement in the 11 o'clock direction). During the passive movement, the KINARM exoskeleton moved the arm in a 'desired' direction, which was toward the location that corresponded to the target position after they were rotated 30^o clockwise around the start circle. The details about the video and passive training were introduced in the following paragraphs. Subjects were divided evenly into four groups: control (CO), full algorithm (FA), partial algorithm (PA), and minimal algorithm (MA) groups. Each block consisted of 4, 8, and 20 observation trials (i.e., the model performed reaching movements 4, 8, and 20 times) for the

MA, PA, and FA groups, respectively. The CO group did not experience any observation or passive trial in the training session. The testing session for the MA, PA, and FA groups consisted of 40 cycles (160 trials) of active reaching movements, during which the 30^o counterclockwise rotation was imposed to the position of the cursor. The CO group only performed 20 cycles of reaching movements in the testing session.

Video of the Model Performance

In the CO group, eight neurologically intact subjects performed the reaching task under the condition in which the display of the cursor was rotated 30^o around the start circle in the testing session. Among those subjects, the one who demonstrated the most representative learning curve of visuomotor adaptation (i.e., this subject's learning curve resembled best the average learning curve obtained from all subjects) was selected as the model to be used for observation. The subjects in the MA group observed 32 trials of reaching movements performed by the model, which indicated progressive improvements in performance (e.g., trials 1, 6, 11, 16 (in block 1); trials 21, 26, 31, 36 (in block 2)). The four trials within each block represented movements made in all four directions. Those in the PA group observed 64 trials of reaching movements performed by the model, which also indicated progressive improvements in performance (e.g., trials 1, 3, 5, 7, 9, 11, 13, 15 (in block 1); trials 21, 23, 25, 27, 29, 31, 33, 35 (in block 2)). Those in the FA group observed all 160 trials of reaching movements performed by the model (i.e., 20 consecutive trials within each block), during which complete adaptation to the visuomotor rotation occurred. The video was replayed for each subject in the FA, PA and MA groups in a way that provided a top-down view of the subject's arm movement from the start circle to the target, along with the movement of the cursor representing the altered hand-path under the visuomotor rotation.

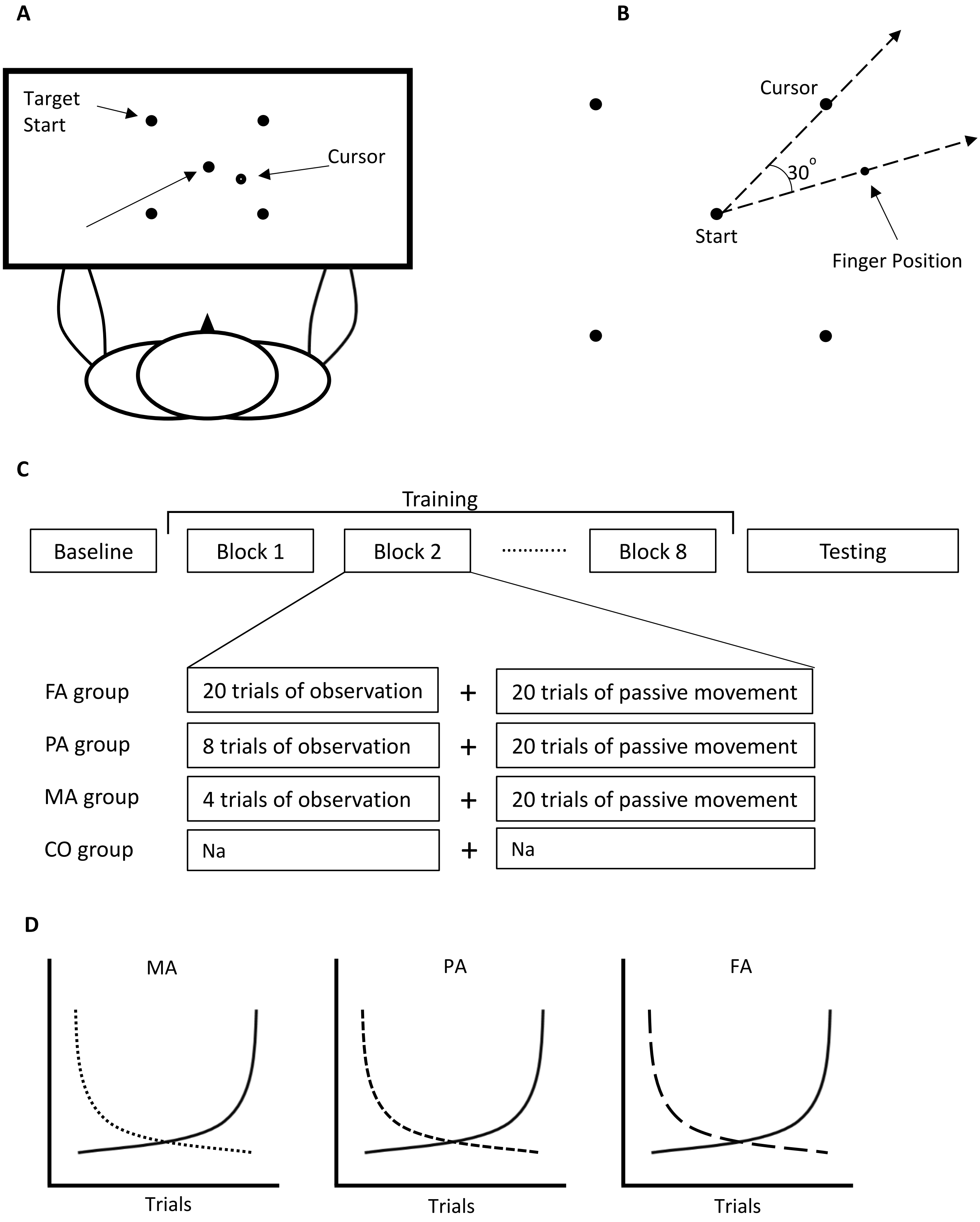
A
Target
Start
Cursor
B
Cursor
30°
Start
Finger Position
C
Training
Baseline
Block 1
Block 2
Block 8
Testing
FA group
20 trials of observation
+
20 trials of passive movement
PA group
8 trials of observation
+
20 trials of passive movement
MA group
4 trials of observation
+
20 trials of passive movement
CO group
Na
+
Na
D
MA
PA
FA
Trials
Trials
Trials

Figure 2.2: (A) Visual display of target, cursor, and start circle. (B) Setup for visuomotor rotation. The position of the cursor is rotated 30^{o} counterclockwise about the position of the index finger, so the subject needs to reach towards the direction that is 30^{o} clockwise about the target. (C) Experimental protocols for Experiment 1. The training session contains eight blocks, while each block contains observation and passive training. The number of observation trials depends on the group. (D) Manipulation of algorithmic learning. We assume that the number of observation trials influences the amount of algorithmic learning (dashed lines). The shorter dash line indicates less algorithmic learning, and long dash line indicates more algorithmic learning.

Passive Movements by the KINARM Exoskeleton

During passive reaching movements, the KINARM exoskeleton moved the arm from the start circle to the locations that were associated with a 30^{o} clockwise rotation of the four targets. The movement delivered by the exoskeleton consisted of a bell-shaped velocity profile; and the peak amplitude of the tangential velocity and the movement duration were determined based on the parameters obtained during active reaching movements of the subjects in our previous studies (Lei, 2016; i.e., the mean value of parameter across all baseline trials was used to program the passive movement). The subject who experienced passive movements was instructed to keep their arm muscles relaxed and not to resist or assist the motion induced by the KINARM exoskeleton. After each trial, the subject moved their hand to the start circle by themselves. Visual feedback of the hand position was not provided during passive movements. This setup for passive movement training enabled the subject to experience the proprioceptive inputs that were associated with the desired movement trajectories (i.e., trajectories to be experienced only following complete adaptation to the 30^{o} counterclockwise visuomotor rotation) without having to generate corresponding motor commands, and also without visual inputs associated with the desired trajectories.

Data Analysis

In order to determine the performance accuracy, the direction error of each trial was calculated by the angular difference between a vector from the start center to the target and another vector from the hand position at movement start to that at peak tangential velocity (Figure 2.2B). In addition, the rate of learning in the testing session was calculated for each subject by fitting the direction errors of the initial 80 trials of the testing session to the following exponential formula:

$$\text{errors}[n] = A * \exp(- r * n) + B,$$

where n was the trial index, A and B were two coefficients, and r was the learning rate. Direction errors from the testing session were subjected to a repeated-measures ANOVA with group (CO, FA, PA, and MA) and cycle as independent variables to determine if there were differences between the subject groups across the cycles in the testing session. Following that, a one-way ANOVA was conducted to compare the learning rate r during the testing session to determine if differences existed among the four groups.

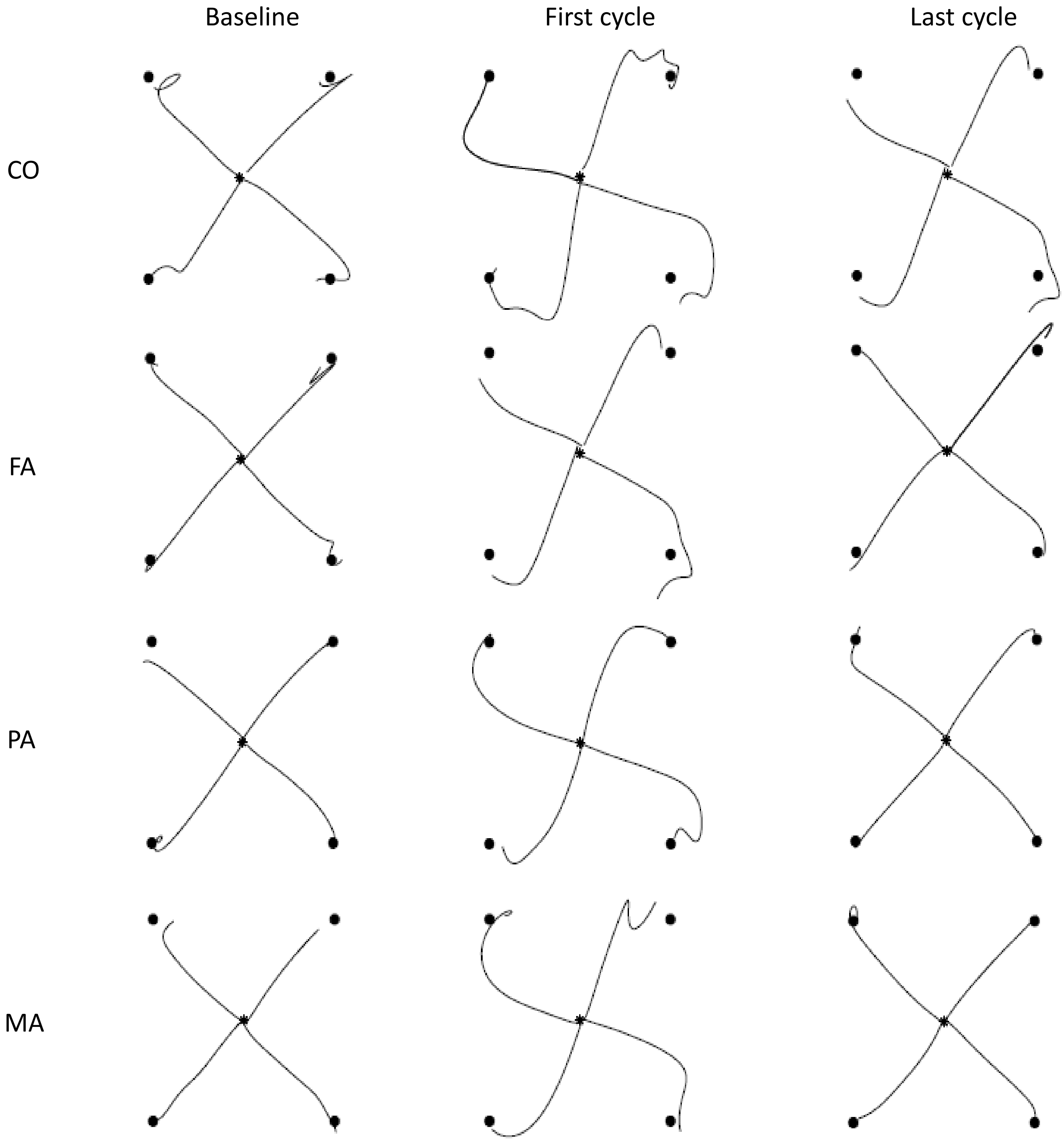

Figure 2.3: Hand-paths from representative subjects from each group in the baseline session (left panel), the first cycle of the testing session (mid panel), and the last cycle of the testing session (right panel).

Results

In this experiment, all the subjects practiced reaching movement during the baseline session. After eight blocks of observation and passive training, they actively adapted to the visuomotor rotation in the testing session. Figure 2.3 illustrated representative hand-paths from the baseline and the testing sessions. The hand-paths of the subjects tested in the FA group were relatively straighter compared to the PA, MA, and CO groups in the initial phase of the testing session. This difference was expected, giving that subjects in FA have experienced more observation trials in the training session. By the end of the testing session, all subjects, except for the ones from the CO group, exhibited straighter and more accurate hand-paths than those observed at the beginning of the session, indicating that they were able to compensate for the systematic perturbation by the end of the testing session.

Figure 2.4 depicted the changes in performance across cycles during the baseline and testing sessions for all four groups. The errors at the beginning of the testing session were

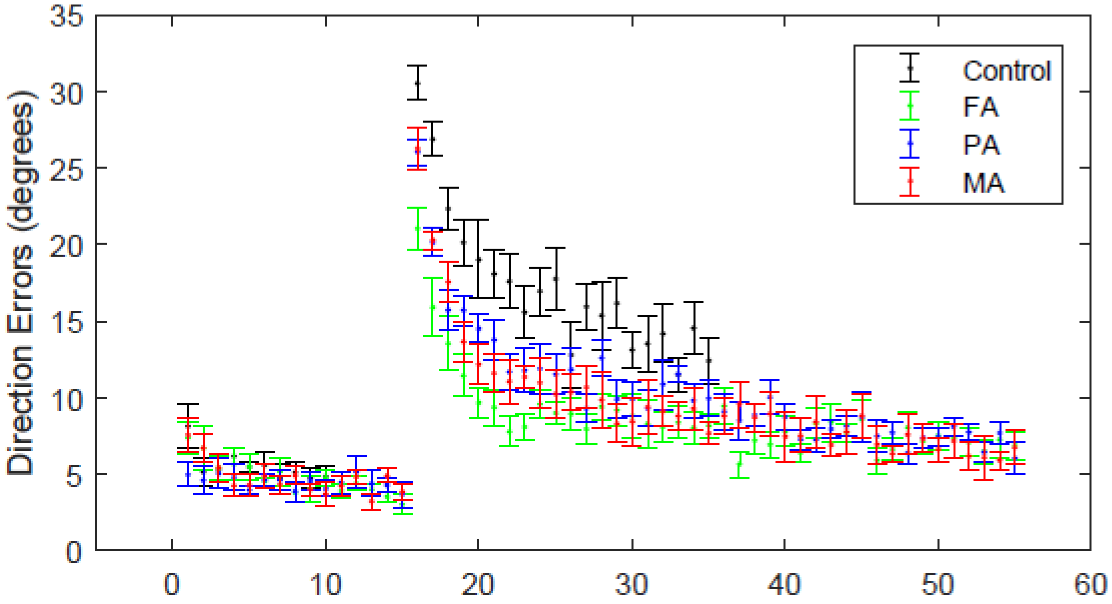

Figure 2.4: Direction errors across cycles in the baseline (Cycle 1~15) and testing (Cycle 16~55) sessions. Every data point shown on X axis represents the mean value of one cycle across subjects in each group (mean ± SE).

substantial but reduced progressively in the subsequent cycles. Repeated-measures ANOVA showed a significant interaction effect between group and cycle on the direction errors in the testing session (F(57,513)=1.556, p =0.008), indicating that the patterns of performance changes across the cycles varied among the four groups in this session. Post hoc analysis using the direction error data from the first cycle revealed that errors observed in the FA group (21.02 ± 1.31, mean ± SE) were significantly lower than those of the PA (26.04 ± 0.82), MA (26.27 ± 1.32) and CO (30.52 ± 1.11) groups ($p < 0.01$). The errors in the PA and MA groups were not significantly different from each other ($p = 0.89$), but they were both lower than the CO group ($p < 0.013$; Figure 2.5A). The learning rates in the testing session were displayed in Figure 2.5B. A one-way ANOVA revealed that learning rates differed across groups ($p = 0.03$). The FA group exhibited a higher rate than all the other groups ($p < 0.019$), but the differences among the left three groups failed to reach the significance level ($p > 0.096$).

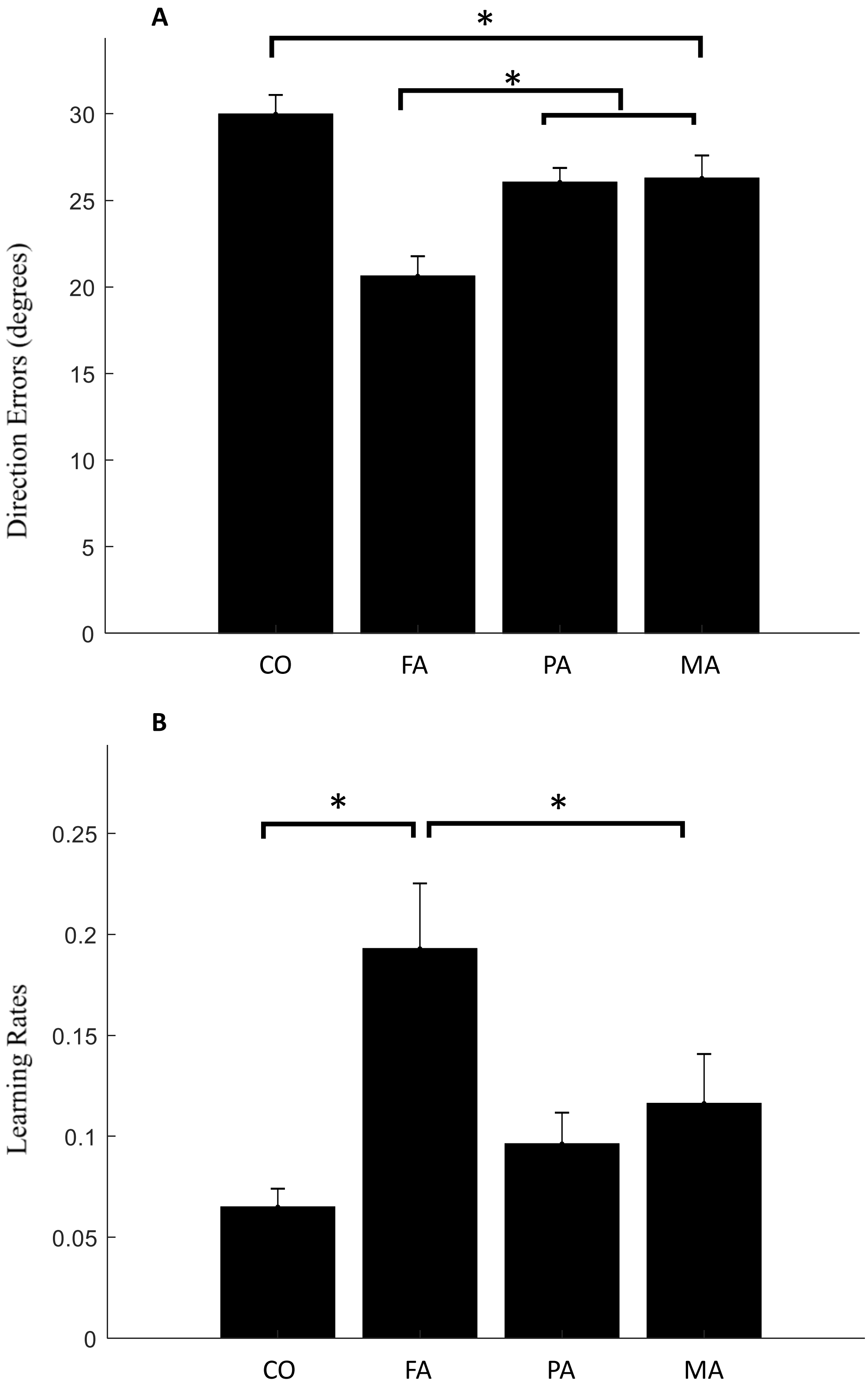

Figure 2.5: (A) Direction errors in the first cycle of the testing session. (B) Learning rates in the testing session. (* $p<0.05$)

Experiment 2

The results from Experiment 1 suggested that the extent of visuomotor adaptation was influenced by algorithmic learning. The purpose of Experiment 2 was to investigate the effects of varying degrees of instance-reliant learning on visuomotor adaptation when the number of observation trials remained the same.

Materials and Methods

Participants

A total of thirty-two (18 males and 14 females) neurologically intact right-handed individuals participated in this study, including 16 subjects who had been tested in Experiment 1. The data from these 16 subjects (8 and 8 in the CO and FA groups, respectively) were reused in Experiment 2 since the tasks for these two subject groups were identical to those in Experiment 1. The inclusion and exclusion criteria were the same as those in Experiment 1. According to our previous studies, the sample size of thirty-two subjects (four groups, eight per group) was large enough to meet the most stringent statistical requirements and allows room for possible attrition.

Apparatus

The same apparatus used for Experiment 1 were used in this experiment.

Experimental Protocol

The fundamental protocol for this experiment was similar to that introduced in Experiment 1, in that the subjects were required to make swift and straight reaching movement with the right arm to one of the four targets displayed in pseudorandom orders. The experiment consisted of three sessions: baseline, training, and testing (Figure 2.6A). The baseline session contained 20 cycles (80 trials) in which the veridical position of the right index finger was projected onto the virtual display as a round cursor. The training session consisted of eight blocks, and each block included both observation training and passive training. Subjects were randomly assigned to one of four groups (Figure 4B): control (CO), full instance (FI), partial instance (PI), and minimal instance (MI) groups. Within each block, the subjects in the FI group observed 5 cycles (20 trials) of reaching movements performed by a naïve model, and then experienced 20 trials of reaching movements passively by the KINARM exoskeleton; the subjets in the PI group observed 20 trials of reaching movements and experienced 8 trials of passive reaching movements; and those in the MI group observed 20 trials of reaching movements and experienced only 4 trials of passive reaching movements. Visual feedback was not provided during passive movement training. The subjects in the CO group did not experience any observation or passive training in this session. For the FI, PI, and MI groups, the testing session consisted of 40 cycles (160 trials) of reaching movement, during which the 30^o counterclockwise rotation was provided; but for the CO group, the testing session had only 80 trials.

Data Analysis

Direction errors were measured to estimate the accuracy of performance. Learning rates were calculated by fitting the direction errors from the initial 80 trials of the testing session to an exponential formula. Direction errors in the testing session were subjected to a repeated-measures ANOVA with group (CO, FI, PI, and MI) and cycle as independent variables to determine if the patterns of adaptation were different among the four groups across the cycles. Following that, a one-way ANOVA was conducted to compare the learning rates during the testing session among the four groups.

Data from the current experiment was also compared to that of Experiment 1. Two one-way ANOVAs were conducted with group as the independent variable to determine whether the direction error and the learning rate were sensitive to either algorithmic or instance-reliant learning.

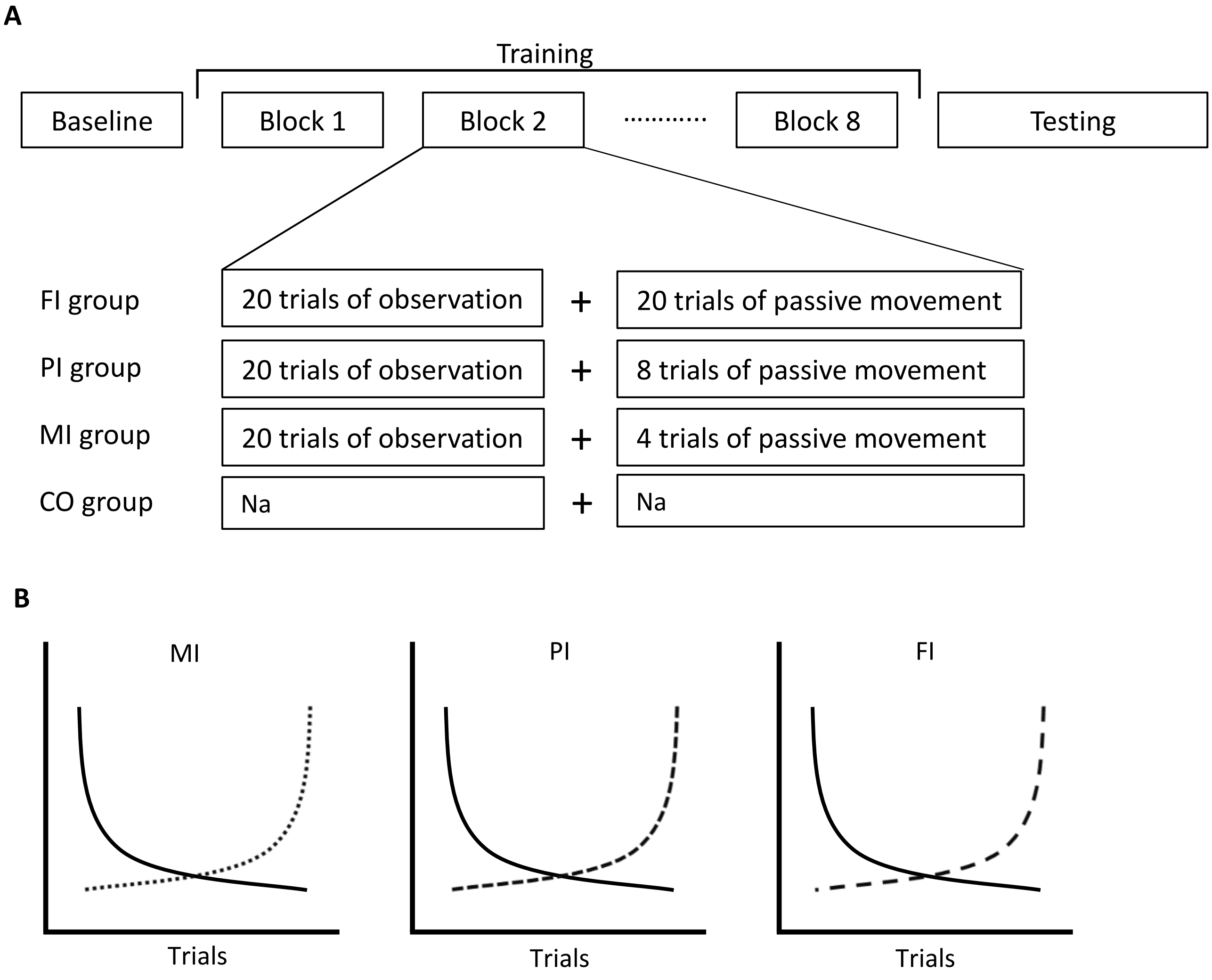

Figure 2.6: (A) Experimental protocols for Experiment 2. The training session contains eight blocks, while each block contains observation and passive training. The number of passive training trials depends on the group that the subject belongs to. (B) Manipulation of instance-reliant learning. We assume that the number of passive training trials influences the amount of instance-reliant learning (dashed lines). The shorter dash line indicates less instance-reliant learning, and long dash line indicates more instance-reliant learning.

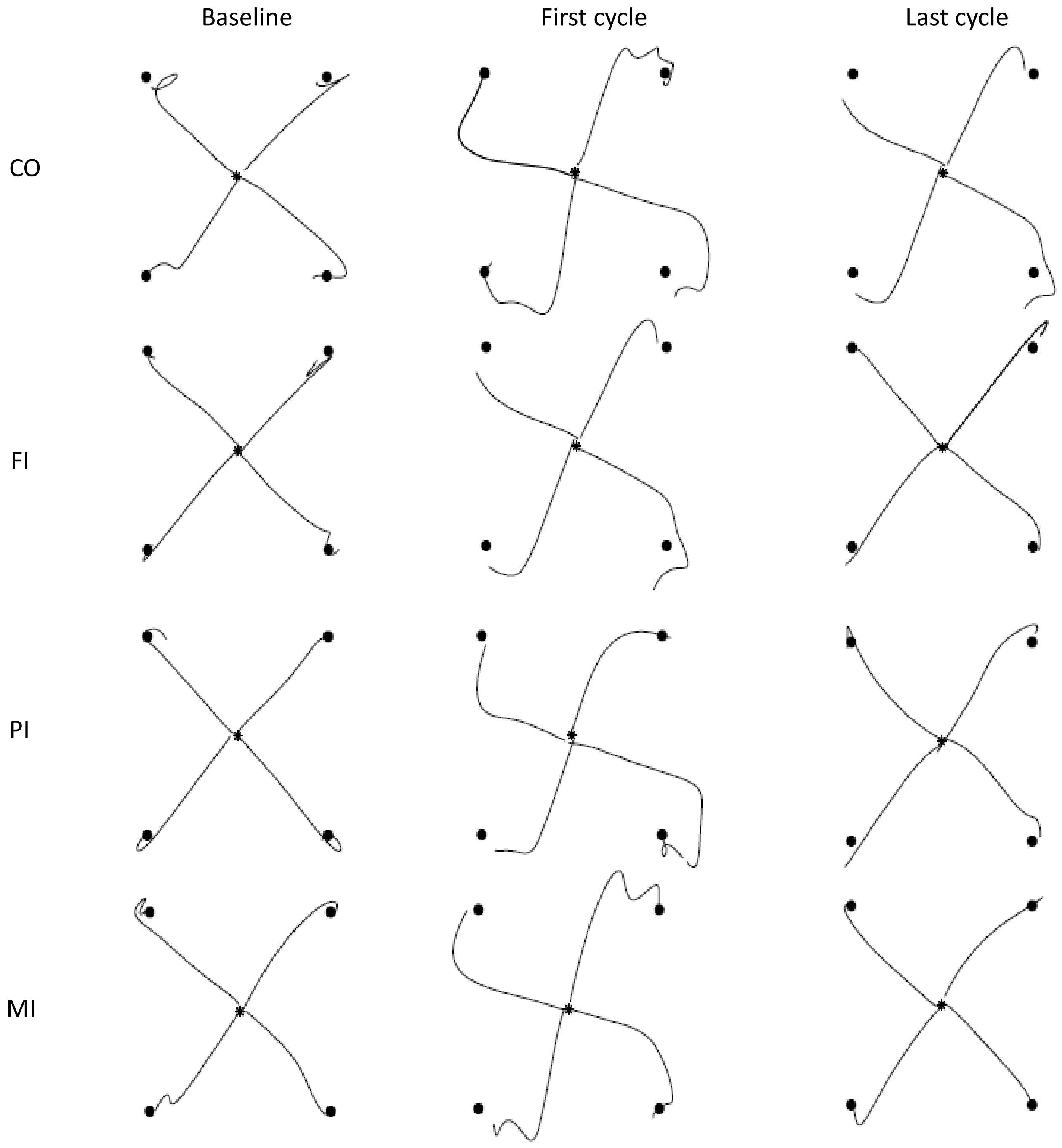

Figure 2.7: Representative hand-paths of the four groups in the baseline (left) session, and the first (mid) and last (right) cycles of the testing session.

Results

Figure 2.7 illustrated representative hand-paths in the baseline and the testing sessions. The hand-paths of the FI group at the first cycle of the testing session were relatively straighter compared to other three groups, indicating that subjects who experienced more passive training trials performed better at the beginning of the testing session. The CO group exhibited the most curved paths at the beginning of the testing session, which was expected since they did not experience any observation or passive training. All the subjects, except for the ones from the CO group, showed relatively straighter hand-paths at the last cycle, indicating that they had adapted to the visuomotor rotation by the end of the testing session.

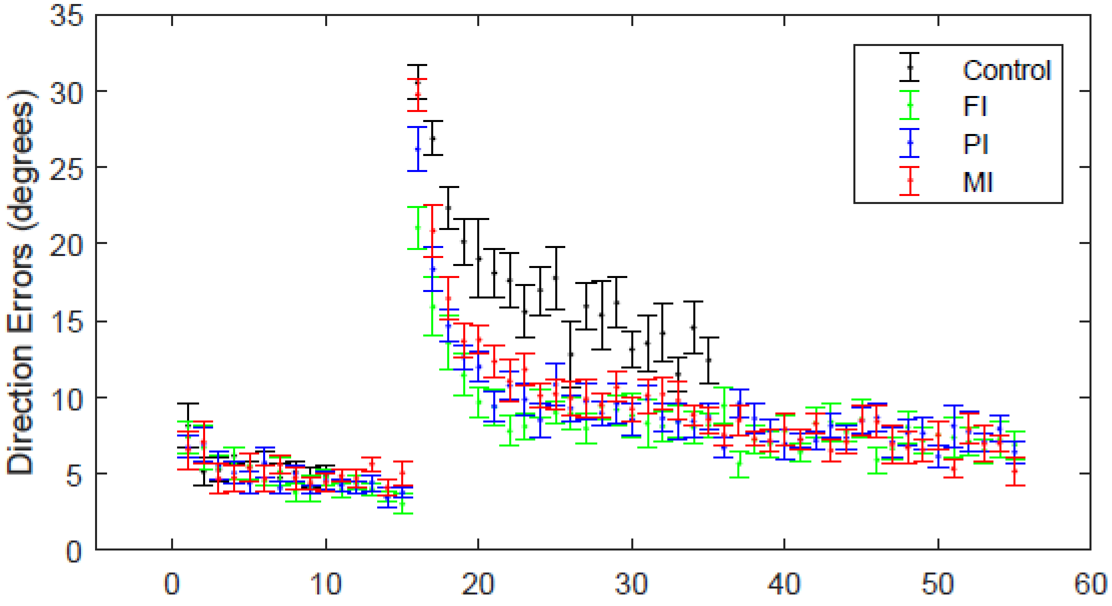

Figure 2.8: Performances of each group in the baseline (Cycle 1~15) and the testing (Cycle 16~55) session. Each data point shown on X axis represents the mean value of one block across subjects in each group (mean ± SE)

Figure 2.8 depicted the changes in performance across cycles during the baseline and testing sessions for all the four groups. A repeated-measures ANOVA revealed a significant interaction effect between group and cycle on the direction errors in the testing session ($F(57,513)=1.681$, $p =0.002$), indicating that the patterns of performance changes across the cycles varied among the four groups. Post hoc analysis using the direction errors from the first cycle of the testing session revealed that errors of the FI group (21.02 ± 1.31, mean ± SE) were significantly lower than those of the PI (26.18 ± 1.45), MI (29.75 ± 1.02), and CO (30.52 ± 1.11) groups ($p < 0.01$; Figure 2.9A). The errors in the PI were lower than the CO ($p = 0.034$) and MI ($p = 0.045$) groups, but the differences between CO and MI did not reach the significance level ($p = 0.896$). A one-way ANOVA analysis showed that the learning rates of the four groups were different in the testing session ($p = 0.043$; Figure 2.8B). The CO group exhibited a lower rate than the other three groups ($p < 0.031$), and the rates of the other three groups are not different from each other ($p > 0.65$).

Figure 2.10A showed the direction errors of the first cycle from Experiment 1 and 2. One-way ANOVA suggested that the direction errors were different across groups ($p < 0.001$). Post hoc analysis revealed that the errors of groups PA and PI were similar ($p = 0.936$), but the group MI exhibited larger errors than MA ($p = 0.043$).

Figure 2.10B showed the learning rates from Experiment 1 and 2. The values of errors differed across groups according to the outputs of one-way ANOVA ($p = 0.012$). The learning rate of group PI was higher than that of PA ($p = 0.026$), and the rate of MI tended to be higher than that of MA, but the difference was not significant ($p = 0.19$).

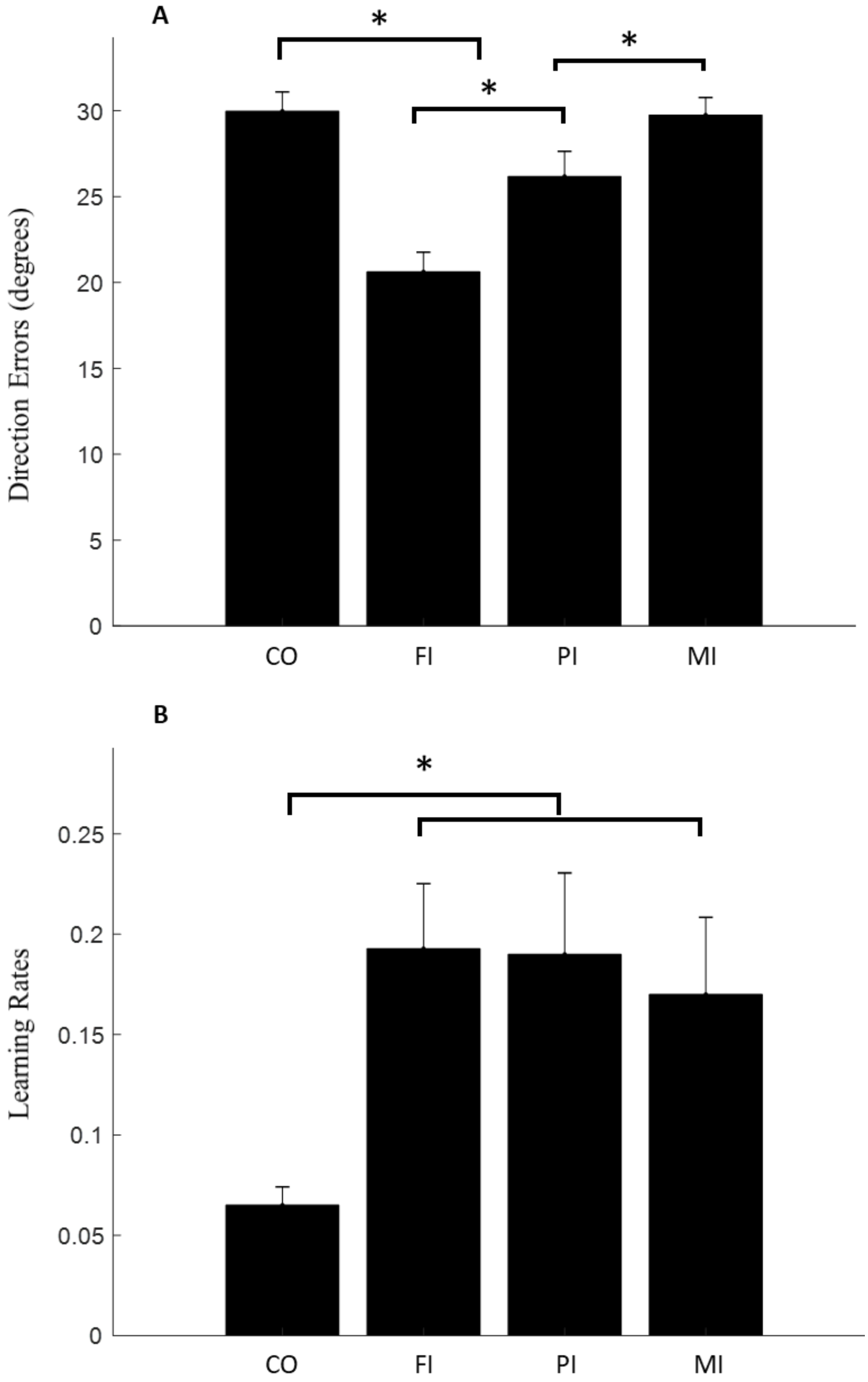

Figure 2.9: (A) Direction errors in the first cycle of the testing session. (B) Learning rates in the testing session. (* $p<0.05$)

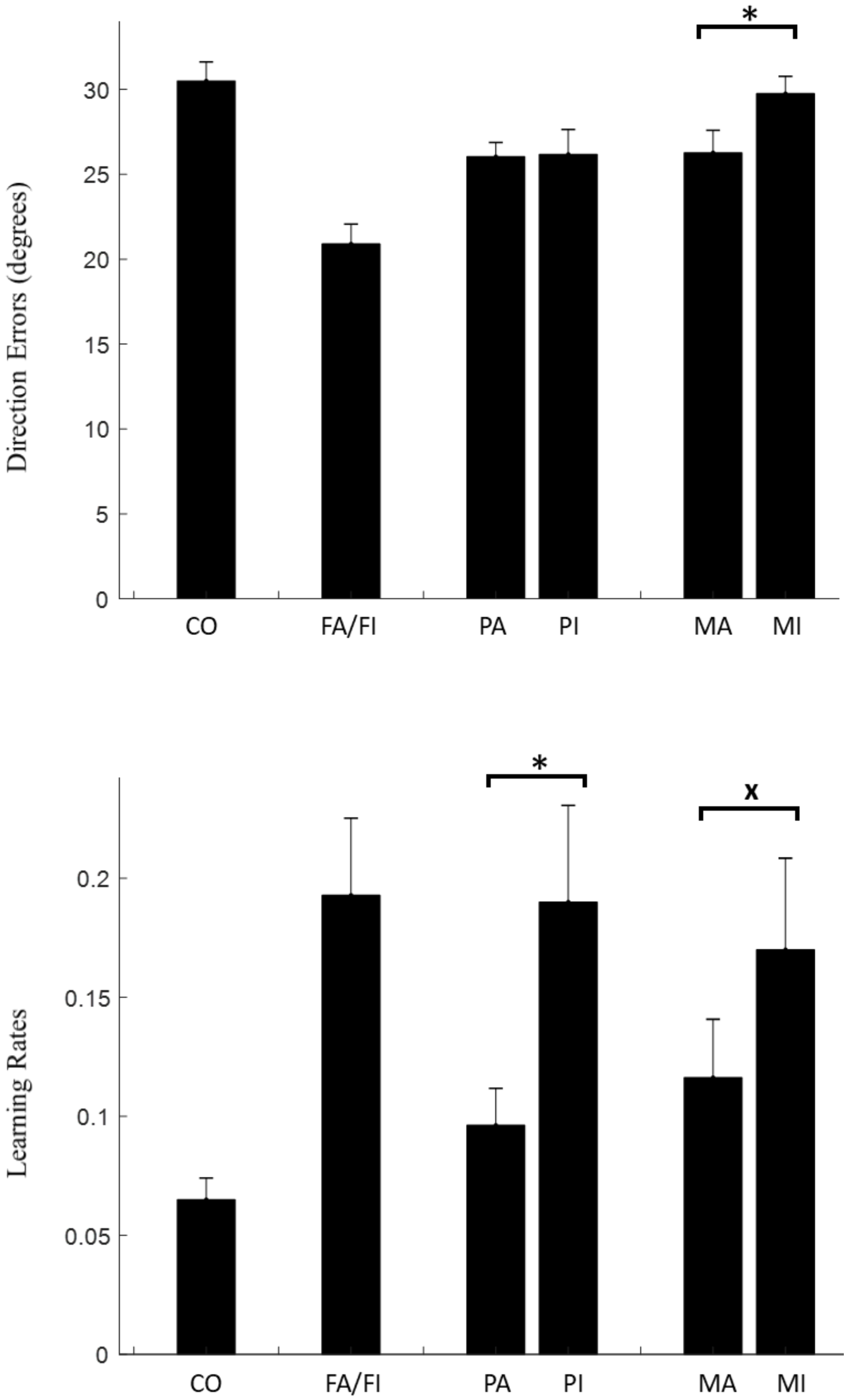

Figure 2.10: Comparing the direction errors (A) and learning rates (B) from Experiment 1 and 2. (* $p<0.05$, ^{x} $p<0.20$)

Discussion

In this study, we investigated the relative contributions of algorithmic and instance-reliant learning to visuomotor adaptation. For this aim, we replaced the active movement training with observation and passive movement training and examined their training effects on subsequent visuomotor adaptation. In Experiment 1, the numbers of observation trials ranged from 32 to 160 in total, while the passive training remained the same (160 trials). The subjects who experienced more observation (e.g., FA group) exhibited greater improvements than the others in the testing sessions, which was consistent with our expectation that the degrees of algorithmic learning influenced the extent of visuomotor adaptation. We also noticed that the performances of the subjects in the PA group who experienced 64 trials of observation were no better than those in the MA group who only experienced 32 trials of observation.

Our findings from Experiment 1 are generally compatible with those reported in the previous studies that investigated the effects of observation learning on motor adaptation (Lei et al., 2016; Mattar & Gribble, 2005). In both Lei's (2016) and Mattar's (2005) studies, observation learning generated substantial but incomplete learning effect, that is, the direction errors were reduced by approximately 30%. However, in another study made by Ong (2010), the errors were reduced by over 70%, which was very different from our findings. Such a large improvement in Ong's study might be due to the effect of using explicit knowledge acquired during observation. In our two experiments, we told the subjects not to think too much about the movement tasks, and did not provide them with any information about the visuomotor rotation through verbal instruction. In this way, explicit processes occurred, but they might not have influenced the movement output significantly (Wang et al. in review). In Ong's study, however, 40% of the subjects were aware of the rotation and applied cognitive strategies to compensate for the visuomotor perturbation. In addition, Ong reported that the subjects did not exhibit any aftereffects after the observation, which is in agreement with the finding reported by Benson (2011) that the subjects who intentionally applied explicit strategies to counterbalance the visuomotor perturbation exhibited little aftereffect after adaptation. Based on the discussion above, we assume that the difference between the present study and Ong's study may be attributed to the additional influence of explicit strategies.

In Experiment 2, we examined the extent of adaptation while the numbers of passive trials were manipulated from 32 to 160 in the training session, but kept the observation trials unchanged (160 trials). The subjects who experienced more passive movement training (FI group) exhibited greater improvements in the testing session than those from group PI, which in turn showed better performances than the ones in group MI. This result supports our hypothesis that the formation of visuomotor adaptation varies as a function of the degrees of instance-reliant learning.

The outputs of Experiment 2 are generally comparable to the previous studies (Wang et al., 2015; Lei et al., 2016, 2017; Diedrichsen et al., 2010; Cressman & Henriques, 2010; Sakamato & Kondo, 2012, 2015) that repetitive practice of the same tasks bias the subsequent performance to the previously trained pattern. Compared to Cressman's (2010) and Sakamato's (2012, 2015) studies, our current study showed less improvement after passive training. For example, subjects from the PI and MI groups exhibited greater direction errors than that in Sakamato's two studies; and the FI subjects who experienced the combination of 160 trials of observation and passive training showed similar improvements compared to the subjects who only experienced passive training in Sakamato's studies. We attributed the differences among these studies to the contribution of visual feedback. In our current study, to inhibit algorithmic learning, visual feedback was removed during passive movement training. However, in Sakamato's two studies, the arm/hand position was visually rotated by 30^o and displayed on the screen. This setup provided sensory feedback errors to the CNS, which could enable algorithmic learning during passive movement training.

By comparing the data from Experiment 1 and 2, we found that observation and passive trials had different effects on the learning rates. Here, we attempt to fit our data to the two main theories on learning rate or savings. The term savings refers to the phenomenon of faster relearning when the CNS encounters the same environmental condition (Smith et al., 2006; Kitago et al., 2013). In some studies, it is suggested that savings emerges from the recall of motor memory that has been consolidated during the preceding training (Huang et al., 2011; Kitago et al., 2013). In these studies, the procedure of adaptation is divided into a fast process that is in charge of reducing the performance errors, and a slow process during which the movement skill is consolidated. If this theory works, the slow process, which corresponds to the instance-reliant learning in our study, should be the main factor that leads to savings. However, the subjects in the FI group did not exhibit higher learning rates than the PI and MI groups, indicating that the learning rate was not sensitive to instance-reliant learning.

Another theory suggests that savings is caused by model-based learning which enables the CNS to reduce the performance errors quickly in the early stage of adaptation (Hadjiosif & Smith, 2013; Haith et al., 2015; Huberdeau et al., 2015; Morehead et al., 2015). In our two experiments, the learning rate is sensitive to the number of observation trials, so our finding is compatible with this theory. As introduced in Chapter 1, model-based, or algorithmic, learning refers to the mechanism in which the visuomotor correlation transform is updated, and it has been thought to involve an implicit process (Mazzoni & Krakauer 2006; Benson et al., 2011;

Wang et al., 2011). However, in recent studies (e.g., Hadjiosif & Smith, 2013; Taylor et al., 2014, 2015; Haith et al., 2015; Huberdeau et al., 2015), explicit learning is also considered as an essential component of algorithmic learning. For example, Haith reported that by excluding the explicit process from model-based learning, the phenomenon of savings ceased in his study (Haith et al., 2015). This result not only suggests that explicit process is essential but also attributes the phenomenon of savings to the explicit component of algorithmic learning. In our experiments, declarative knowledge about the reaching task was delivered to the subjects during the observation, so the faster learning in the subsequent testing session could be due to either the explicit process or the implicit algorithmic process.

In our two experiments, the outcomes of observation are positively associated with the number of trials, and the effect of observation can be superimposed to the passive training. This finding suggests that action observation has clinical applications, for example, some researchers suggest that observation can be included in the treatments for patients who attempt to restore motor functions after stroke (Buccino et al., 2012, 2013; Ertelt et al., 2007; Bassolino et al., 2014). In these studies, observation of daily actions is combined with physical training in a program which usually lasts for a few weeks. Based on the limited literature reports, patients usually exhibited more improvements than the control group who only receive physical training during the same time, which means that action observation has additional impacts on the recovery of motor functions (Buccino et al., 2012; Ertelt et al., 2007).

Compared to active training, observation or passive training is less efficient to achieve the same outputs, so active training might always be the first choice for neurologically intact people; but for patients who suffer from neurological diseases, observation and passive training might be their only choice. Therefore, it will be useful to find out why they are not as efficient as active training. Here, we present two potential reasons: first, the sensory feedback loop is not sufficiently activated by movement observation and passive training, so that the algorithmic learning might be partially inhibited in our study. This assumption is somewhat analogous to the finding reported by Beets (2012), who compared the active and passive training effects on a bimanual coordination task. In his study, active training and passive training resulted in comparable outputs in the testing session, but if visual feedback was provided to the subjects during the test, active training generated much better outputs. This study suggests that the neural substrates corresponding to error detection/correction are more involved when the subjects voluntarily practice the movement tasks.

Another reason is that the CNS is less devoted to learning during observation and passive training. According to neuroimaging studies, the substrates for observation, passive training, and active training are highly overlapped in cortical areas (Macuga & Frey, 2012; Filimon et al., 2007; Eaves et al., 2016; Malfait et al., 2010; McGregor & Gribble, 2015), but the neurons within M1/S1, SMA, and cerebellum are more activated during active training (Macuga& Frey, 2012; Jaeger et al., 2014; Sahyoun et al., 2004; Ciccarelli et al., 2005; Mehta et al., 2012). Lower activation indicates that the CNS is not concentrated during the learning; therefore, we might try to increase the neural activation in our future studies in order to augment the outputs of observation and passive training.

Summary

In this study, we examined the relative contribution of algorithmic and instance-reliant learning to visuomotor adaptation. Both of the learning processes were positively associated with improvements in the subsequent performance, and these two processes could be added up to achieve better outputs. These findings confirm our hypothesis that algorithmic and instance-reliant learnings make independent contributions to the adaptation. Moreover, we expect that these training methods can be more efficient in the future, and can be finally applied to clinical regions to help individuals who suffer from neurological disorders.

CHAPTER 3: Motor Control of Movement Magnitudes

In this and the next chapters, the nature of instance-reliant learning is investigated. We have discussed that instance-reliant learning is movement specific and effector specific, which suggests that the extent to which instance-reliant learning can generalize across conditions may be quite limited (Wang et al., 2015; Bao et al., 2017; Lei et al., 2016, 2017). In this chapter, we continue to investigate the nature of instance by examining if instance-reliant learning is also magnitude specific.

Introduction

In the past two decades, visuomotor adaptation has been widely used to investigate the acquisition and storage of motor learning (Wang & Sainburg 2003, 2004; Wang et al., 2015; Tseng et al., 2007; Krakauer 2009; Huang et al., 2011; Kitago et al., 2013; Palluel-Germain et al., 2011). The typical visuomotor adaptation involves a rotated visual display of the target and the cursor, requiring the CNS to remap the visuomotor relationship, especially the directional differences, between visual and proprioceptive inputs (Shadmehr & Wise, 2005). Meanwhile, there is another kind of visuomotor adaptation in which the subject learns to change the scaling factor in performance (Bock, 1992; Pine et al., 1996; Krakauer et al., 2000; Pearson et al., 2010). In this setup, the distance between the cursor and the start circle is multiplied by a constant, so the subject needs to adjust the magnitude of his movement to accurately bring the cursor to the target.

Rotation adaptation and scaling adaptation each correspond to distinct learning processes, as they exhibit different properties in learning and generalization (Pine et al., 1996; Krakauer et al., 2000). Rotation adaptation is direction-specific, such that the training in a selected direction can only influence the performance within a narrow range (Pine et al., 1996; Krakauer et al., 2000; Yin et al., 2016). For example, if it takes a certain number of trials for a subject to complete the training towards a fixed target, it will take him/her about 8 times of the training to achieve the same level of adaptation if he/she needs to reach towards 8 different targets (Krakauer et al., 2000). By contrast, scaling adaptation is direction independent. It can generalize to other directions and workspaces completely, and there is no difference in mental effort to adapt to one or more targets (Bock, 1992; Pearson et al., 2010; Krakauer et al., 2000; Yin et al., 2014). Reasons leading to the differences between these two adaptations are still under research, but it is widely accepted that the direction and magnitude of the reaching movement are governed by different mechanisms (Krakauer et al., 2004; Rosenbaum, 1980).

The neural substrates involved in rotation adaptation include large areas around the cerebellum, posterior parietal cortex, and premotor cortex (Wang & Sainburg, 2004; Criscimagna-Hemminger et al., 2010; Ramnani 2006; Diedrichsen et al., 2005; Seidler & Noll, 2008; Ghilardi et al., 2000, Tseng et al., 2007); however, recent neuroimaging studies suggest that only the putamen and cerebellum are activated during scaling adaptation (Krakauer et al., 2004; Palluel-Germain et al., 2011; Seidler, 2013; Turner et al., 2003). Therefore, the neural programming for the direction might be more complicated as it demands co-working of much more cortical networks. This idea is compatible with a behavioral study which showed that the time needed for a human subject to determine the movement direction is much longer than the time needed to consider the movement magnitude (Rosenbaum, 1980), indicating that it costs more calculation work for the CNS to determine the movement direction as compared with the magnitude.

The purpose of the study in this chapter is to determine whether the movement instance is magnitude specific. As will be mentioned in the Discussion session, Krakauer has conducted a study in which the generalization of rotation adaptation across magnitudes was investigated. In that study, he had the subjects practicing reaching movements with magnitudes of 7.2 cm and tested the generalization to 2.4, 4.8, and 9.6 cm. The main concern of that study was that the 7.2 and 9.6 cm were very close, so the movement instances were not quite different no matter they were magnitude specific or not. In this study, we adjusted the magnitudes of reaching performance to 1 and 10 cm and re-tested the generalization across magnitudes. If the movement instance was magnitude specific, the extent of generalization would not be complete.

Experiment 3

Materials and Methods

A total of thirty-two neurologically intact right-handed individuals participated in this study. The criteria for inclusion and exclusion were the same as Experiment 1 and 2. According to our previous studies, the sample size of thirty-two subjects (four groups, eight per group) was large enough to meet the most stringent statistical requirements and allowed room for possible attrition.

During the experiment, the participant was seated in front of the experimental setup, as shown in Figure 3.1A. The height of the chair could be adjusted to fit the participant’s height. Center-out reaching movements were performed horizontally across a digitizing touchpad (Intuous 3; Wacom, Ageo, Saitama, Japan). The trajectory of the performance was sampled by a digitizing pen incorporated to the touchpad. Position of the subject’s hand was projected onto a 1280 x 1024 pixel resolution LED which was mounted horizontally 20 cm above the touchpad, so direct vision of the hand and the digitizing mouse was blocked by the LED as shown in Figure 3.1A. A computer program developed using software Presentation (Neurobehavioral Sys., Albany, CA) was used to control the visual stimulus and also to record the trajectory of reaching movement on the surface plane of the touchpad. The experimental data were processed using Matlab (MathWorks, Natick, MA).

The subject was asked to perform rapid reaching movements with the right arm by moving a cursor (2 cm in diameter) from a start circle to one of four targets (2 cm in diameter) that were distributed evenly across a circle with a 10 cm radius which was centered on the start circle of the reaching movement. The reaching tasks included two types of movements: full reach (FR) and partial reach (PR) (Figure 3.1B). In the FR condition, the subject needed to complete the whole reaching task from the start circle to the displayed target. In PR condition, they only made small-magnitude reaching movements (1 cm) within the dashed circle (right panel of Figure 3.1B), but the cursor would continue to move along the direction of the mouse until the distance it had traveled was 10 cm (i.e., the distance between the start and target).

The experiment consisted of three sessions: baseline, adaptation, and transfer. Each session consisted of 20, 40, and 40 cycles of reaching movements, respectively. Within each cycle, the four targets at the directions of 45^o, 135^o, 225^o and 315^o were displayed in a pseudorandom order. The baseline session, during which the cursor indicating the location of the hand was veridical, contained 20 cycles (80 trials in total) of reaching movement. In the adaptation and transfer sessions, the subject adapted to a visual display that was rotated 30^o counterclockwise about the start circle (i.e., hand movement made in the “12 o’clock” direction resulted in cursor movement made in the “11 o’clock” direction). The subjects were divided evenly into four groups in these two sessions (Figure 3.1C): PR-FR group, FR-FR group (as a control group compared to PR-FR), FR-PR group and PR-PR group (as a control group compared to FR-PR). In the adaptation session, subjects in the FR-PR and FR-FR groups performed reaching movement under FR condition; those in the PR-FR and PR-PR groups performed reaching movement under PR condition. In the transfer session, subjects in PR-FR and FR-FR groups performed movement under FR condition; subjects in FR-PR and PR-PR groups performed movement under PR condition.

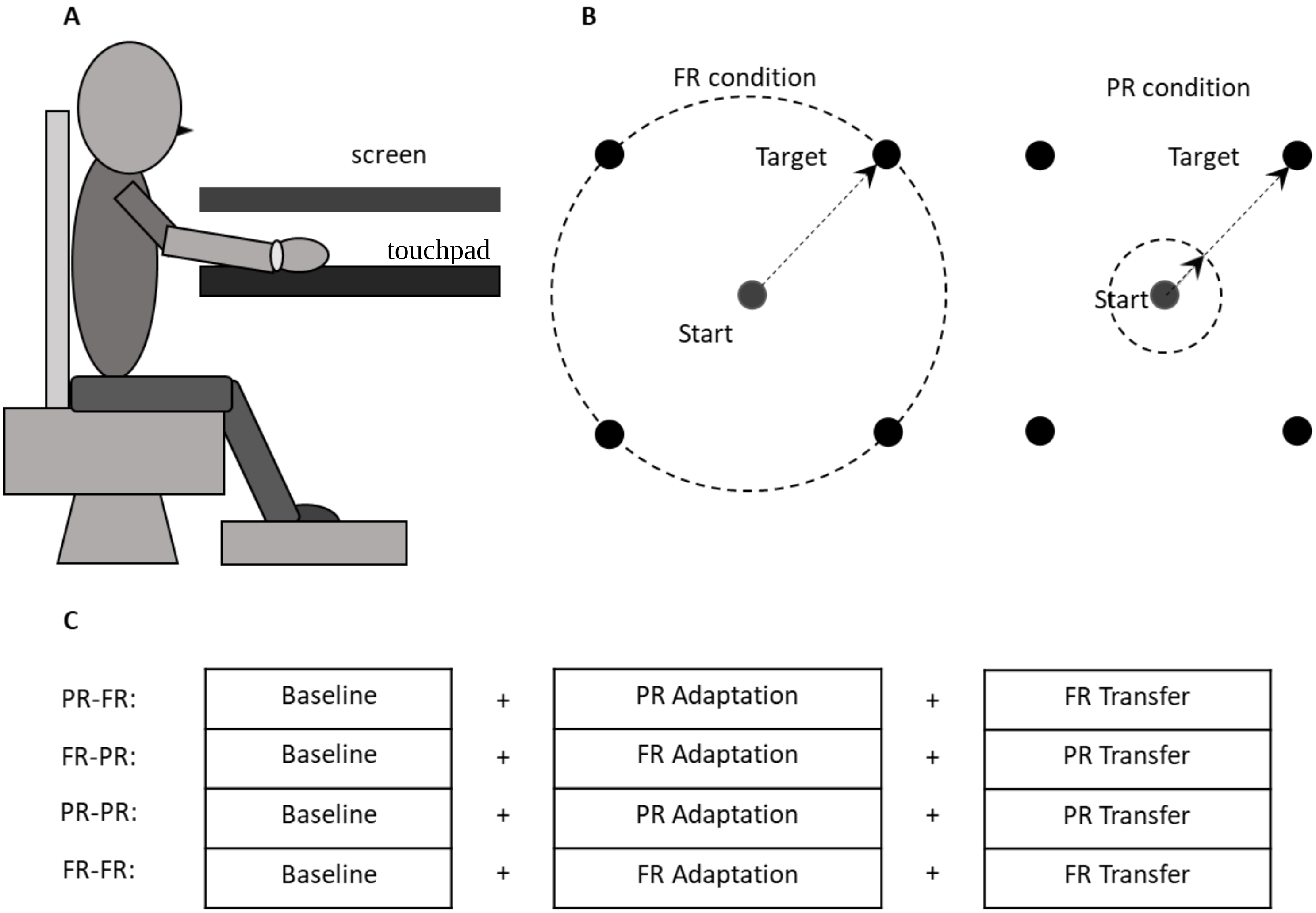

Figure 3.1: (A) Experimental setup of the reaching movement. The position of the hand is projected to the screen as a round cursor. (B) Setup for FR and PR reaching. In FR condition, the subject moves the mouse from the start position to the target; in PR condition, the subject only moves onto the dashed ring, and the cursor continues to reach out following the same direction. (C) Experimental protocol Experiment 3. After the baseline session, subjects are divided into PR-FR, FR-PR, PR-PR, and FR-FR conditions based on the magnitudes of tasks in the adaptation and transfer sessions.

Data Analysis

Direction errors of reaching movements were measured to examine the performance accuracy. Using this measure, the extent of transfer from the adaptation session to the transfer session was also calculated for each subject based on the following equation: [(error at the first cycle of the adaptation session – error at the first cycle of the transfer session) / (error at the first cycle of the adaptation session – error at the last cycle of the adaptation session)] × 100%. The learning rate in the transfer session was calculated for each subject by fitting the direction error data to an exponential function.

Direction errors from the adaptation and transfer sessions were subjected to two repeated-measures ANOVA with group (PR-FR, FR-PR, FR-FR, and PR-PR) as a between-subject factor and cycle as a within-subject factor. Following this, two one-way ANOVAs, with group as a between-subject factor in both ANOVAs, were conducted: one to compare the learning rates in the transfer session across the groups, and the other to compare the extent of transfer across the groups. The alpha level was set at 0.05 for ANOVA and post hoc comparisons [Fisher's least significant difference (LSD) tests for between-group comparisons].

Results

The representative hand-paths from each group were illustrated in Figure 3.2. In the baseline session (Fig 3.2, first column), the hand-paths extended straightly from the start to the targets in all the four conditions, indicating that the reaching movement was not difficult for the subjects to perform when veridical visual feedback was provided. In the first cycle of the adaptation session, the subjects exhibited trajectories that deviated from the target directions (second column); but they moved straight to the target by the end of the adaptation session (third column), indicating that they adapted to the visuomotor rotation condition. In the first cycle of the transfer session, subjects all showed relatively straight and accurate hand-paths except for the group PR-FR. This result suggested that the generalization from FR reaching to PR was almost complete, but the generalization from PR to FR was limited.

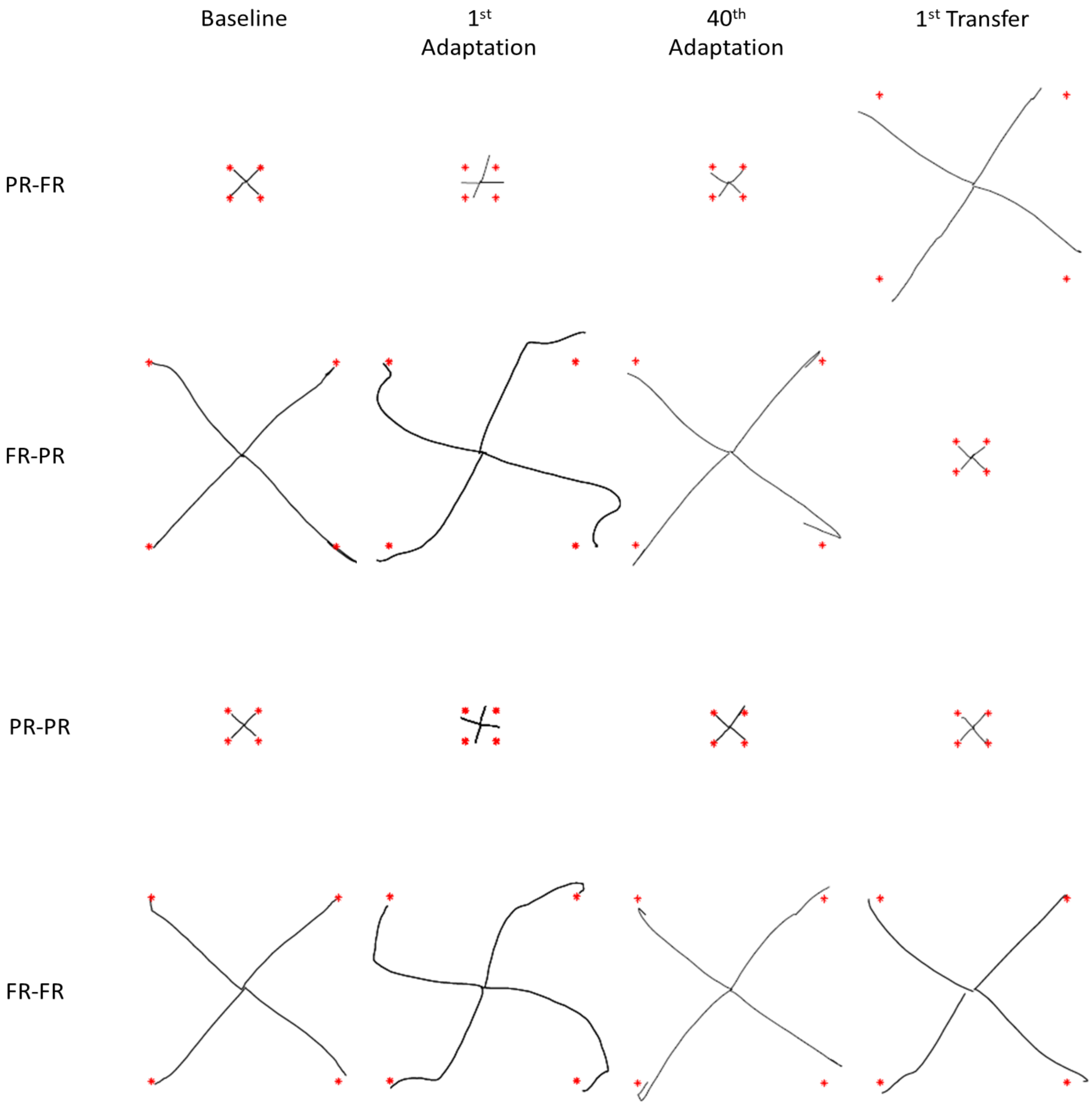

Figure 3.2: Hand-paths from representative subjects from each group (separated by row) in the baseline session (first column), first and last cycles of the adaptation session (second and third columns), and the first cycle of the transfer session (fourth column).

Direction errors across the cycles were displayed in Fig 3.3. In the adaptation session, direction errors decreased gradually from 30.9 ± 1.6 (mean ± SE) to 7.6 ± 1.8 degrees. Repeated-measure ANOVA suggested that the performances of the four groups were similar ($F(3, 27) = 0.533$, $p = 0.663$). In the transfer session, a repeated-measure ANOVA revealed a significant interaction effect between the cycle and the group ($F(3,27) = 5.747$, $p = 0.004$). Post hoc analyses using the errors of the first cycle indicated that the PR-FR subjects exhibited larger errors than the other three groups in the first cycle (M2F = 19.9 ± 1.5 degrees; $p < 0.001$), while the other three groups were not statistically different from each other ($p > 0.15$; Fig 3.4A).

One-way ANOVA revealed that the extent of transfer from the adaptation to the transfer session was different across groups ($p = 0.012$; Figure 3.4B). Post hoc tests showed that subjects in group PR-FR exhibited lower transfer (~ 50%) compared to the other three groups (~ 100%) ($p < 0.004$), and there was no significant difference between those three groups ($p > 0.714$). Another one-way ANOVA showed that the learning rates were different across the groups in the transfer session ($p <0.05$). Subjects in the PR-FR group exhibited slower rates than others, as shown in Figure (3.4C; $p <= 0.05$).

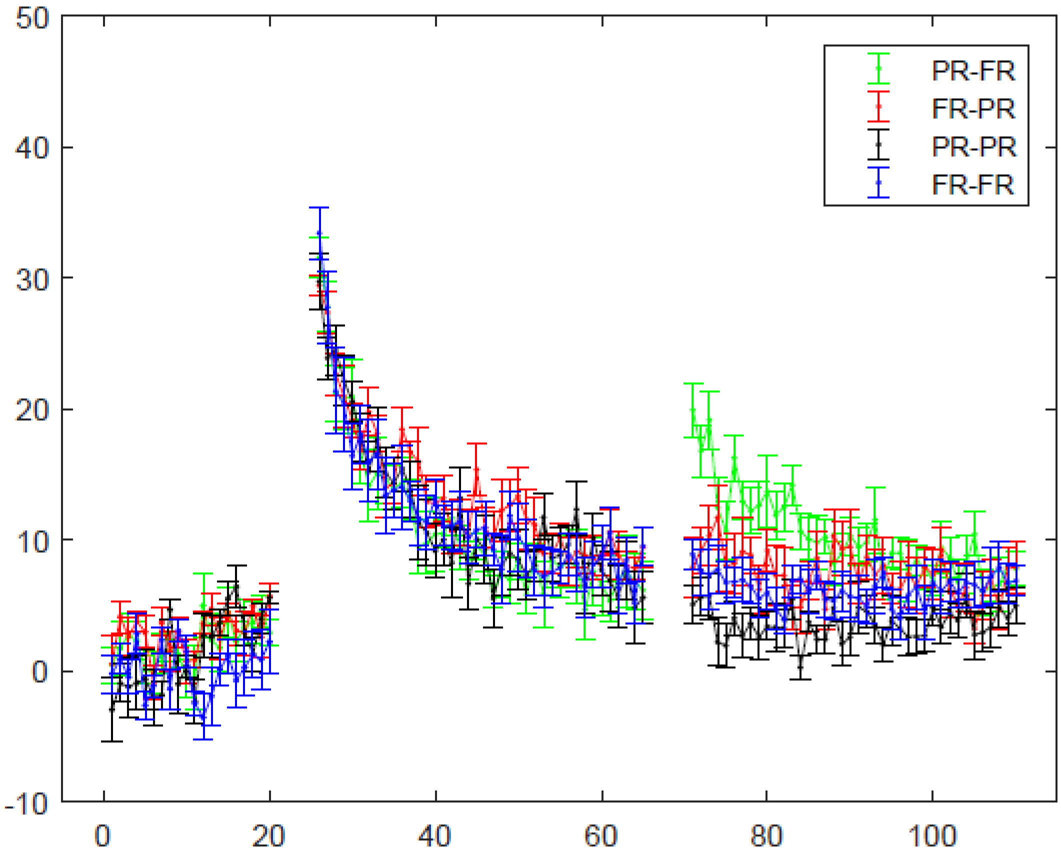

Figure 3.3: Direction errors in the baseline (Cycle 1~20), adaptation (Cycle 21~60), and transfer (Cycle 61-100) sessions. Every data point shown on X axis represents the mean value of one cycle across subjects in each group (mean ± SE).

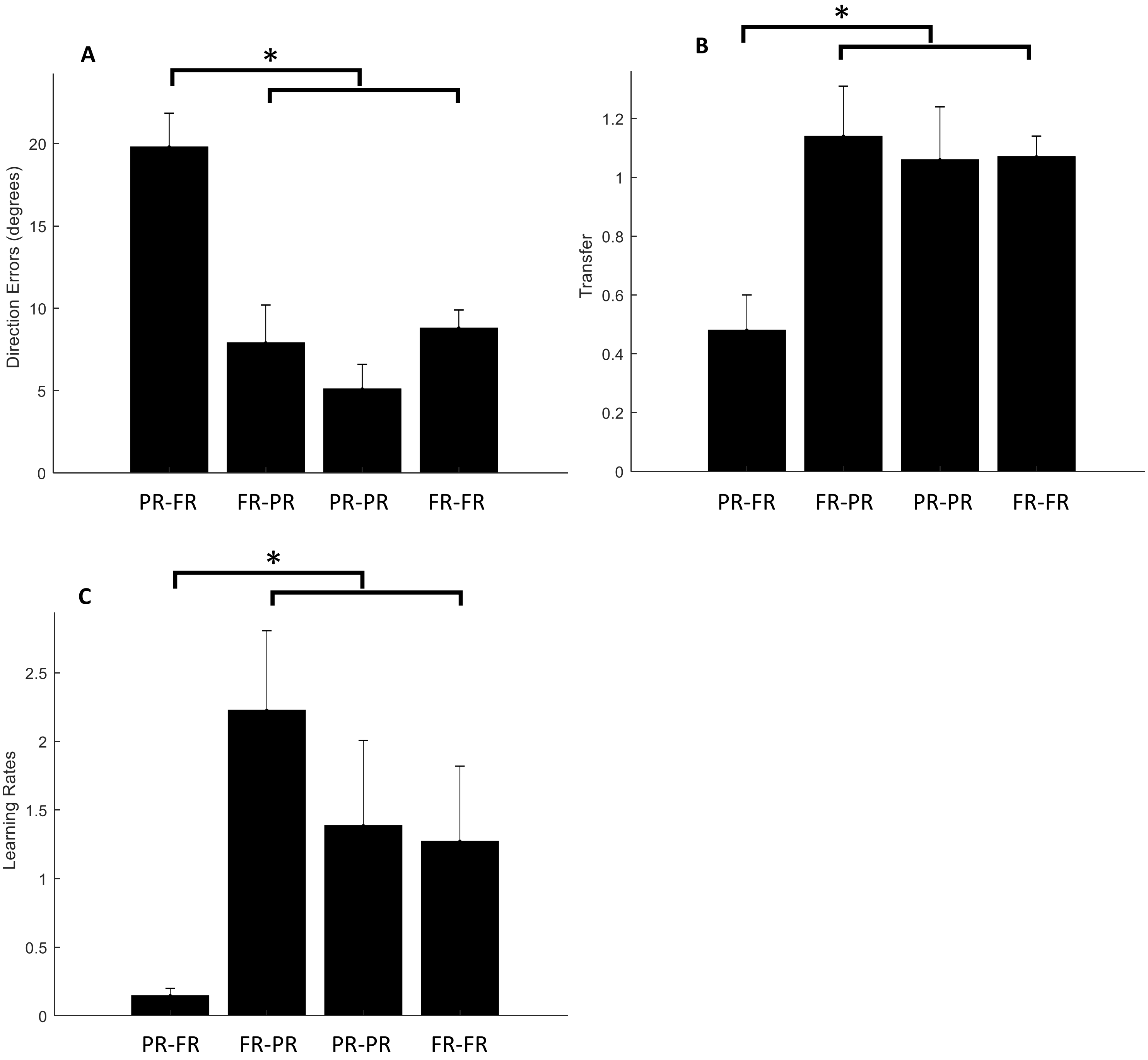

Figure 3.4: (A) Direction errors in the first cycle of the transfer session. (B) Extent of transfer from the adaptation to the transfer sessions. (C) Learning rates of the transfer session. (*p <= 0.05)

Discussion

In this study, we examined whether rotation adaptation could generalize across conditions in which the movement magnitude varied, but the direction remained the same. In the FR condition, the subjects moved for 10 cm to reach the target; in the PR condition, they only made a 1 cm displacement from the start point, while the cursor continued to move for another 9 cm following the same direction. That is, the set up for the PR condition was equivalent to a visuomotor adaptation to a scaling factor of 10. Our results indicated a similar training pattern in the adaptation sessions, no matter whether the magnitude of the movements was large or small. However, the performance in the transfer session was different across groups. The extent of transfer from the large to small magnitudes (group FR-PR) was 100%, but the transfer from small to large (group PR-FR) was limited to about 50%. Given that the movement directions and also the size of visuomotor rotation remained the same between the PR and FR conditions, the limited generalization indicates that the motor memory associated with full reaching movements are not identical to that associated with partial reaching movements, which in turn suggests that motor instances are magnitude specific.

Our data shows that the pattern of generalization varies depending on whether the transfer occurs from small to large movements or vice versa. That is, our current finding of complete generalization from the large to small magnitudes, which replicates the findings of Krakauer et al. (2000), suggests that the neural command required for a large-magnitude reaching movement completely encompasses that for a small-magnitude movement. This is intuitive, considering that while carrying out the large-magnitude movement, most (if not all) movement properties inherent to the small movement (e.g., the range of motion by the involved joints and muscles) will be experienced. Thus, the subjects who experienced FR training could directly make use of the existing control policy to perform PR movements. On the other hand, our finding of limited transfer from the small to large movements suggests that the neural command required for a small-magnitude reaching movement does not involve all the movement parameters required to carry out a large-magnitude movement.

In Krakauer’s study, the subjects practiced reaching tasks with a magnitude of 7.2 cm, and then they performed similar movements with magnitudes of 2.4, 4.8, and 9.6 cm, respectively. The extent of transfer from 7.2 cm movements to 2.4 or 4.8 cm movements was 100%, which was compatible with our findings; but the transfer from 7.2 to 9.6 cm was also 100%, which differs from our data. The main factor to this difference might be the selection of magnitude, that 7.2 cm is too close to 9.6 cm, so the neural control for these two movements might largely overlap (e.g., the range of motion by the involved joints and muscles quite similar between the movements of the two magnitudes). However, in our PR condition, the subjects only needed to move their limbs with limited magnitude and braked quickly when the cursor crossed the dash line (Figure 3.1B, right panel), so they learned to compensate for the visuomotor perturbation by turning towards the direction, but did not move too much along the direction. In this way, the movement instances acquired during PR reaching were not enough to execute PR reaching, so it took the subjects in group PR-FR a few more trials to restore the movement errors to baseline level in the transfer session.

Transfer of adaptation across magnitudes

Vectorial planning hypothesis has been widely used to describe how the CNS executes a target-oriented reaching movement (Gordon et al., 1994; Messier & Krakauer, 1999; Krakauer et al., 2000; Wang & Sainburg et al., 2005). According to this hypothesis, the CNS combines the spatial locations of the hand and the target to form a hand-centered plan which determines the direction and magnitude of the movement trajectory. However, it is interesting that after the initial PR training, the subjects did not just follow the same direction to extend the magnitude, but chose a direction which biased by about 20^o from the desired direction towards the baseline direction. Considering that magnitude and direction are considered to be independently specified in reaching movement (Pellizzer & Georgopoulos, 1993; Krakauer et al., 2000; Bock, 1992; Gordon et al., 1994), it is likely that changes in magnitude should not alter the direction; however, our data clearly shows that when we extend the magnitude (e.g., transfer from PR to FR), the direction was altered.

Here we propose that the movement output is either a result of retrieval of movement instance or a combination of algorithmic learning and instance-reliant learning. In order to achieve fast and automatized control of the movement, the CNS prefers to retrieve the existing instance which has been stored in the preceding training. So when the magnitude switched from 10 to 1 cm for the FR-PR group, the movement instance of FR reaching was already available (Figure 3.5, upper row). Thus, the CNS made use of the FR instance by cutting off the magnitude to 1 cm without changing the movement direction. If the existing instance cannot be directly applied to the subsequent performance, the movement output will be the combination of algorithmic learning and instance-reliant learning. For the subjects in group PR-FR, since movement instances accrued during the adaptation session cannot be used in the transfer session, the CNS could only retrieve the baseline instances (Figure 3.5, bottom row), whose direction was towards the baseline target. However, the algorithmic learning acquired through adaptation session transferred or partially transferred across magnitudes, so the combined movement direction in the transfer session was 20^o away from the desired direction (right panel of the bottom row).

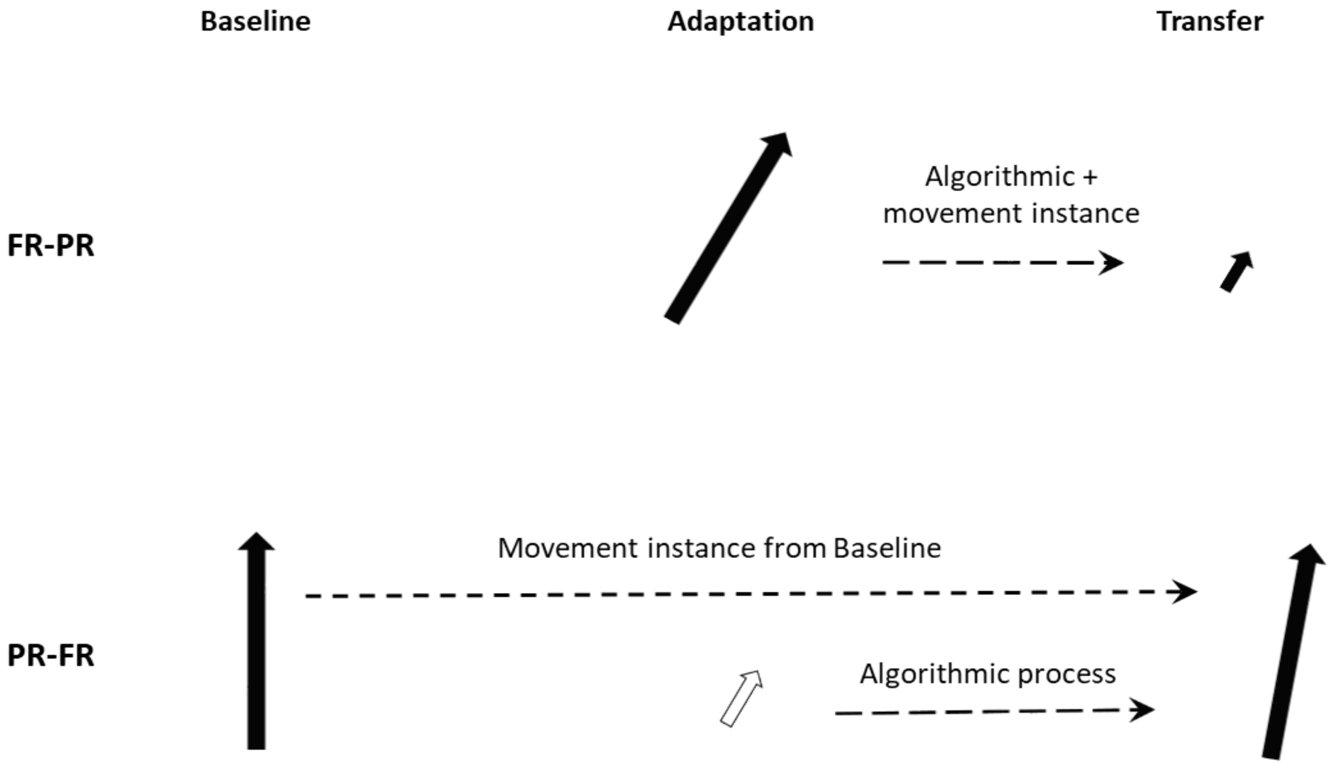

Figure 3.5: Transfer of visuomotor adaptation across magnitudes. (Upper) Transfer from large to small magnitudes. (Bottom) Transfer from small to large magnitudes.

In this study, the transfer of rotation adaptation across magnitudes is about 50%, which is similar to the transfer across limbs and the transfer across directions in the literature and our previous studies (Wang et al., 2015; Bao et al., 2017; Lei et al., 2017; Carroll et al., 2014; Taylor et al., 2011; Pine et al., 1996; Krakauer et al., 2000). We have posited that the reason to the limited transfer is that only the algorithmic learning can transfer across limbs and directions, while the instance-reliant learning is limb- and direction-specific (Wang et al., 2015; Lei et al., 2017). Based on this knowledge, and the findings from this study, we suspect that the effect of algorithmic learning is globalized, while instance-reliant learning is movement specific.

The notion of instance-reliant learning for motor control could involve multiple aspects, such as the generation of motor commands, cutaneous feedback about the environment, coordination of different segments, and the perception of the kinesthetic system (Wang & Sainburg, 2003, 2004). In the current study, the subjects in PR condition missed the experience that they reached the target, so the knowledge of implementing that part was also missing. Therefore, even though they could *shoot* towards the target in PR condition, they could not execute the movement correctly in the subsequent FR task. The most important aspect of movement-specific instance might be the proprioception (Ghez & Sainburg, 1995; Sainburg et al., 1993, 1995, 1999; Lateiner & Sainburg, 2003; Sarlegna & Sainburg, 2009). During the reaching performance, the kinesthetic system, such as cutaneous receptors, Golgi tendons, joint receptors, and so forth, provides information about the motion and the state of limb segments, and enables the CNS to plan the movements that involve multiple limbs and joints (Sarlegna & Sainburg, 2009; Sainburg & Kalakanis, 1999). Animal and clinical studies have provided evidence that proprioception is essential in control and learning. In animal studies (Polit & Bizzi, 1979), Polit and Bizzi reported that monkeys were able to recall the reaching movements after the deafferentation surgery, yet it was challenging to acquire new skills. For human subjects who suffered from severe large-fiber sensory neuropathies (Sainburg et al., 1993; Sarlegna et al., 2006), their performance of reversal movements that involved more than one single joint (e.g., slicing a loaf of bread) was inaccurate and uncoordinated even though they attempted to adjust their control through visual feedback. These studies suggest that proprioception plays a crucial role in joint coordination, so when the proprioception of the reaching task is not available in our

PR task (since they only shoot towards the target), it is not surprising that the transfer from PR to FR is not complete.

Summary

In order to determine whether instance-reliant learning is magnitude specific, we examined the generalization of adaptation across magnitudes. According to our data, the automatized control of movement is strictly restricted to the magnitude it has covered. This finding might be an important supplement to the existing knowledge, and we expect that it could add knowledge to the neural motor control of both direction and magnitude. In the next chapter, the discussion on instance-reliant learning and algorithmic learning will be continued.

CHAPTER 4: Instance-Reliant Learning Is Influenced by Workspace and Limb-Configuration

In Chapter 3, we have shown that the controls of small and large magnitudes are not identical. In this study, we continue to investigate the nature of instance-reliant learning by examining the generalization across conditions in which the workspace location or limb configuration is varied, but the movement direction and magnitude remain the same.

Introduction

Visuomotor adaptation can generalize across workspaces and limb configurations (Heuer & Hegele, 2011; Wang & Sainburg, 2005; Krakauer et al., 2000), but the extent of generalization depends on movement directions. If the direction is the same in the new workspace, subjects do not need to be re-trained for the reaching task; if the direction is not the same, the preceding training has only limited influence on the new direction (Wang& Sainburg, 2005; Heuer & Hegele, 2011; Krakauer et al., 2000). This phenomenon suggests that the remapping of visuomotor coordinates is direction specific, but not workspace specific or limb configuration specific.

Visuomotor adaptation is thought to involve two main processes: algorithmic and instance-reliant learning (Logan, 1988; Wang & Sainburg, 2004; Wang et al., 2015). Considering that visuomotor adaptation is workspace and limb configuration independent, movement instances associated with the adaptation might also be workspace and limb configuration independent. To test this assumption, we designed two experiments in this study to determine if instance-reliant learning could generalize across different workspace locations (Experiment 4), and across different configurations (Experiment 5).

In order to examine the nature of instance-reliant learning, we needed to keep the algorithmic learning part unchanged but manipulated the movement instance during the training. In our previous study, we showed that the extent of generalization across directions could be adjusted by providing movement instances towards the untrained directions (Lei et al., 2017). In that study, subjects practiced reaching towards one target (at direction of 12 o'clock) under the perturbation of 30^o visuomotor rotation, and after every 20 trials, a robotic exoskeleton repeatedly moved the arm towards another direction which was rotated 30^o clockwise away from another target (at the direction of 6 o'clock). After the training, we examined the generalization of adaptation to the second target under the same visuomotor condition, finding that the subjects adapted to the rotation faster in that target direction compared to the control group who did not experience any passive training with the robotic exoskeleton. In the current study, we continued to use this protocol to examine the effect of passive instances on the performance towards the second target. We still had the subjects practice reaching movements towards the 12 o'clock direction, so the algorithmic learning part (practice, adapting to the same rotation) was unchanged across subject groups. But we made changes to the setup of the passive movement training: to determine if the movement instance was workspace specific, the passive training was shifted rightward without changing the direction in extrinsic space (Experiment 4). To determine if the movement instance was limb configuration specific, the limb configuration was altered while the direction and the workspace remained unchanged (Experiment 5). We hypothesized that if the movement instances were not workspace specific or configuration specific, generalization across workspace or limb configuration would not be influenced in either Experiment 4 or 5, respectively.

Experiment 4

In this experiment, we examined the pattern of generalization following visuomotor adaptation across movement conditions in which the direction of movement remained the same, but the workspace location varied.

Materials and Methods

Participants

Thirty-two right-handed subjects (18-35 years old) were recruited via word of mouth or flyers posted on the campus of the University of Wisconsin-Milwaukee. Handedness was assessed using the Edinburgh Handedness Inventory (Appendix C; Oldfield, 1971). The subjects signed informed consent approved by the Institutional Review Board of the University of Wisconsin-Milwaukee (Appendix B) prior to participation and were randomly assigned to one of the four groups in this study (eight subjects per group). After the experiment, they received either a cash bonus or extra credit for their coursework. Exclusion criteria for this study were: (a) the subject was unable to complete assessment due to a low level of consciousness, developmental delay, low literacy, or inability to use English; (b) the subject had a neurological disease or peripheral disorder affecting movement of the upper limbs; (c) the subject had a vision impairment including color-blinded; (d) the subject had a psychiatric diagnosis (e.g., schizophrenia). None of the subjects had participated in any other motor adaptation study within two months prior to this experiment.

Apparatus

The experimental setup was shown in Figure 4.1A. Subjects sat inside the robotic system with arms supported by the exoskeletons that provided full gravitational support. The KINARM was incorporated with a virtual reality system that provided visual stimuli on the horizontal display. During the experiment, direct vision of the arm was blocked by the screen, but a cursor representing the position of the index finger was displayed to guide the reaching movements. The visual stimuli consisted of a start circle (2 cm in diameter) located at the center of the screen and one target circle (2 cm in diameter) which was positioned 10 cm away from the start circle (Figure 4.1B). Movement data were sampled by the exoskeleton at 1000 Hz, low-pass filtered at 15 Hz, and differentiated to yield position and velocity values. The output data were processed using Matlab.

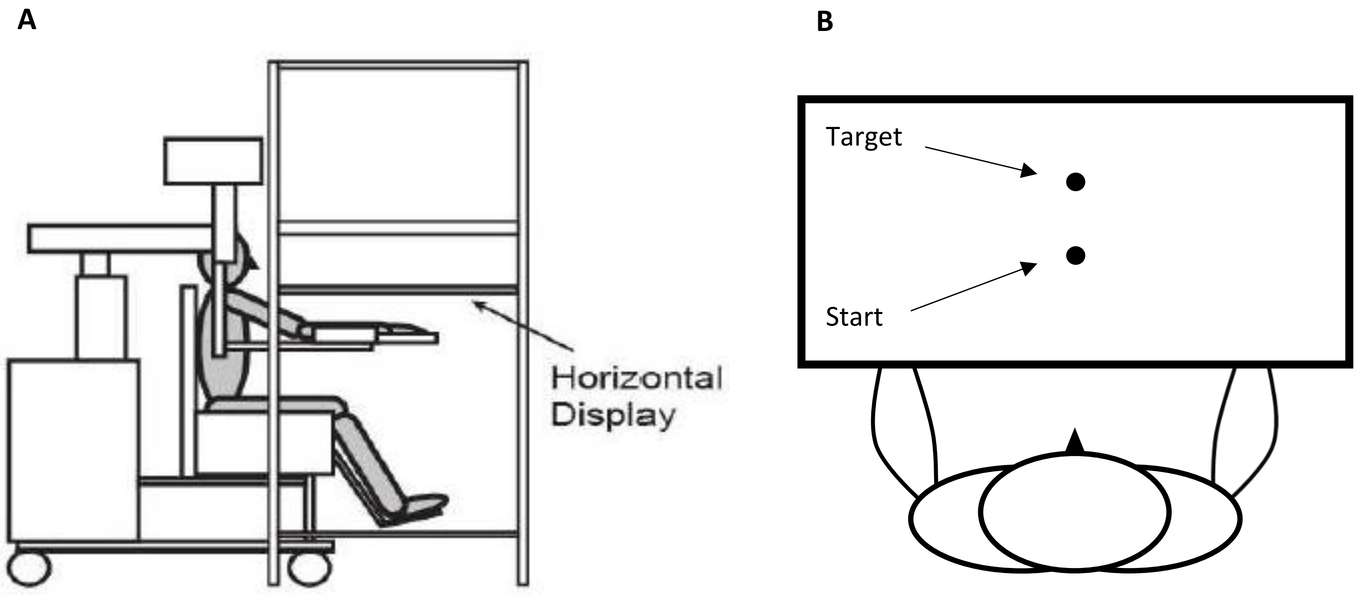

Figure 4.1: A: Experimental setup for Experiment 4. The subject was seated inside the robotic exoskeleton to perform reaching movement. Direct vision of the hand was blocked by the horizontal screen, but visual feedback was provided during the active reaching movement. B: An illustration of the start circle and target circle presented on the horizontal display.

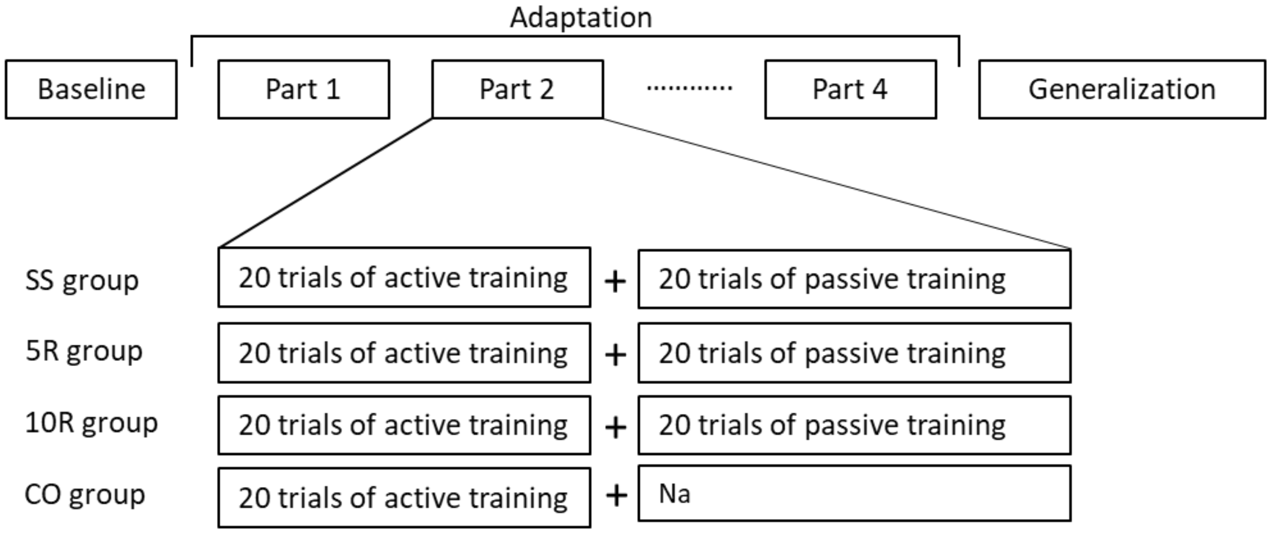

Figure 4.2: Experimental protocol for Experiment 3. The adaptation session is subdivided into four parts, and each part contains both active and passive training except for the CO group.

Experimental Protocol

During the reaching performance, the subjects were instructed to perform swift and straight target-oriented reaching movements from the start position to one of the two targets that appeared 10 cm above (training target) or 10 cm below the start circle (generalization target; Figure 4.3A). The experiment consisted of three sessions: baseline, adaptation, and generalization. Each session included eight blocks (40 trials), 16 blocks (80 trials), and 16 blocks (80 trials) of active reaching movement, respectively (Figure 4.2). In the baseline session, the veridical position of the index finger was provided, so the subjects got familiar with the task by making reaching movement repeatedly towards the training target at the direction of 12 o’clock. The adaptation session was divided into four parts evenly while each part contained four blocks (5 trials per block) of active reaching movement towards the training target. After each part, the robotic exoskeleton KINARM moved the right arm repetitively towards a direction that was 30^{o} rotated clockwise about the generalization target. For this passive training, the subjects were divided into four groups evenly: control (CO) group, same start (SS) group, 5 cm to right (5R) group, and 10 cm to right (10R) group. Subjects from the CO group did not experience any passive training, but they took a short break when others were taking passive training with the robotic exoskeleton. Subjects from the other three groups experienced four blocks (20 trials) of passive reaching within each part. The subjects in SS group experienced passive movements that started from the same start circle used for active reaching movements; the passive movement instances provided to subjects in the 5R group were shifted laterally to the right by 5 cm, and the instances were shifted laterally to the right by 10 cm for subjects from 10R group. Continuous visual feedback was provided during the active arm reaching movements but was removed for the passive reaching. In the generalization session, all subjects actively reached from the same start circle used for active reaching movement towards the generalization target at the direction of 6 o'clock under a 30^o visuomotor rotation.

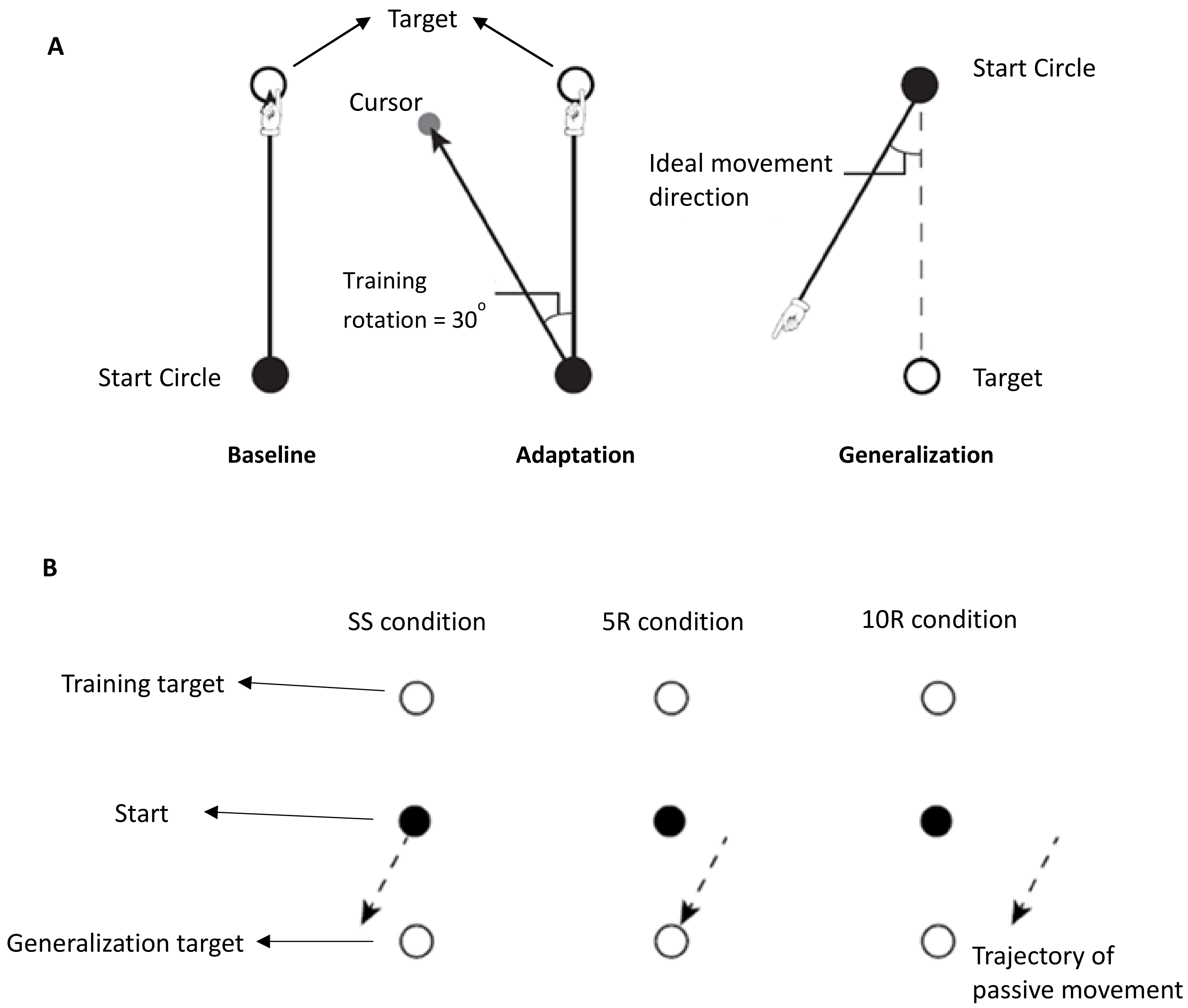

Figure 4.3: Schematic diagram of the reaching movements for Experiment 4. A: Setup for the active reaching performance. Subjects reached towards the training target in baseline and adaptation sessions, and reached toward the generalization target on the opposite side in generalization session. In the adaptation and generalization sessions, the subjects needed to reach toward 30^o clockwise about the target in order to make the cursor reach towards the target. B: Setup for the passive training. The passive movement was represented by the dashed line. It started from the original start position for SS condition; and started from a position that was 5 cm right from the original start position for the group 5R, and started from the position that was 10 cm right from the original position for the group 10R.

Data Analysis

Direction errors from the adaptation session were subjected to a repeated-measures ANOVA with group (CO, SS, 5R, and 10R) as a between-subject factor and block as a within-subject factor to determine if there were differences among the subject groups. Another repeated-measures ANOVA with the same two factors was conducted to determine if the magnitudes of errors were different in the generalization session.

The learning rate in generalization session was determined by fitting the direction error data to an exponential function. The extent of transfer across directions was calculated using the following equation: (errors of the first block in adaptation session – errors of the first block in generalization session) / (errors of the first block in adaptation session – errors of the last block in adaptation session) x 100%. Two one-way ANOVAs with group as the between subject factor were conducted: one was to compare the learning rates in generalization session, and the other was to compare the extent of transfer across conditions.

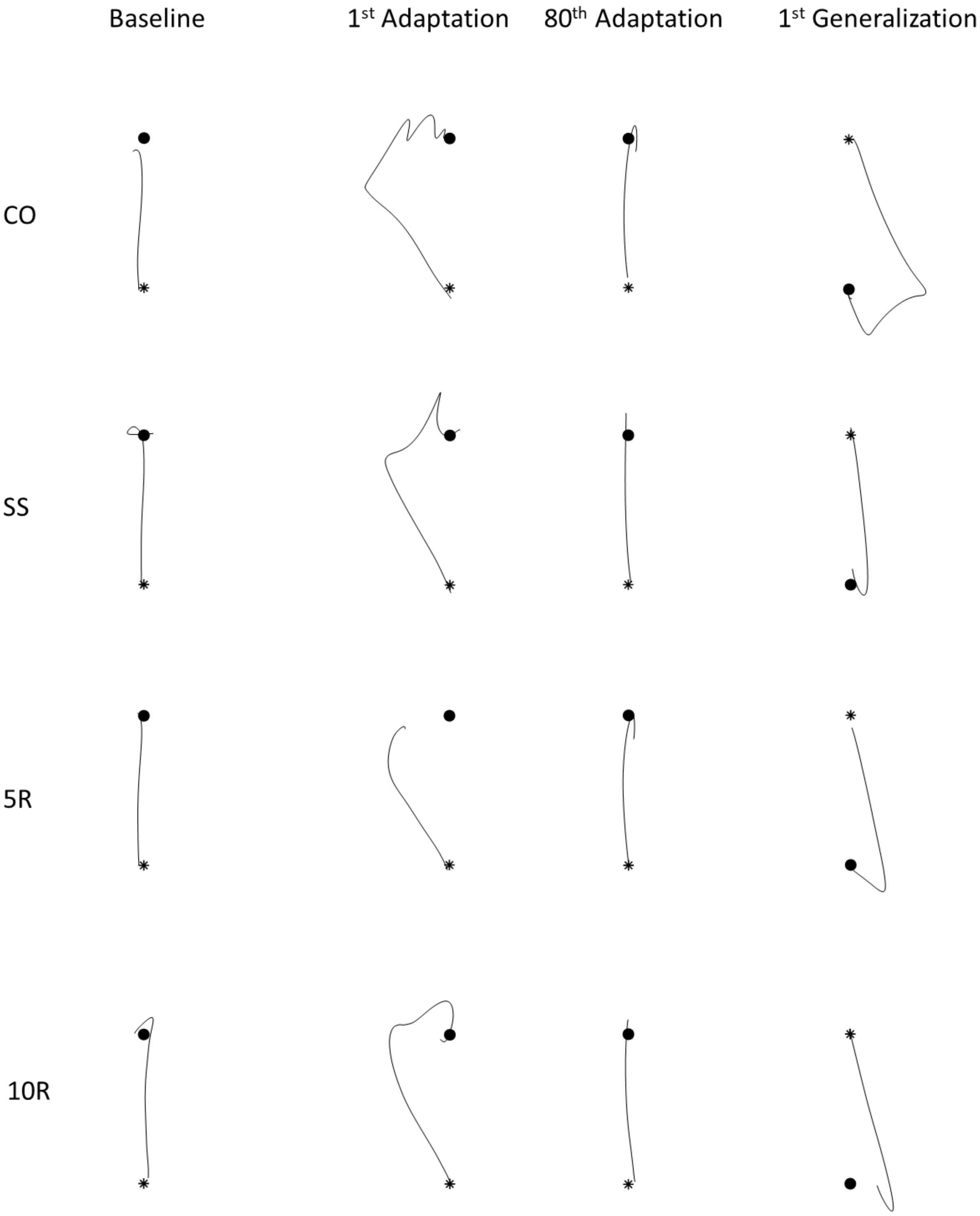

Figure 4.4: Hand-paths from representative subjects from each group (separated by row) in the baseline session (first column), first and last block of the adaptation session (second and third columns), and the first block of the generalization session (fourth column).

Results

Figure 4.4 illustrates the hand-paths of representative subjects from each group for the baseline session, adaptation session, and the generalization session. The hand-paths at the beginning of the adaptation session largely deviated from the target line (second column), but they became relatively straight and accurate by the end of the adaptation session (third column). The hand-paths at the first block in the generalization session were shown in the fourth column. Hand-paths shown for all four groups were largely curved, which indicated that the generalization across directions to the second target was incomplete for all the groups. According to Figure 4.5A, the hand-path of the subject from the CO group was more curved than those of the subjects from the SS, 5R and 10R groups who experienced passive movement training, indicating that the passive training benefited the subsequent performance in the same direction. The hand-path of the group SS subject was relatively straighter than the 5R subject, which in turn was straighter than the 10R subject.

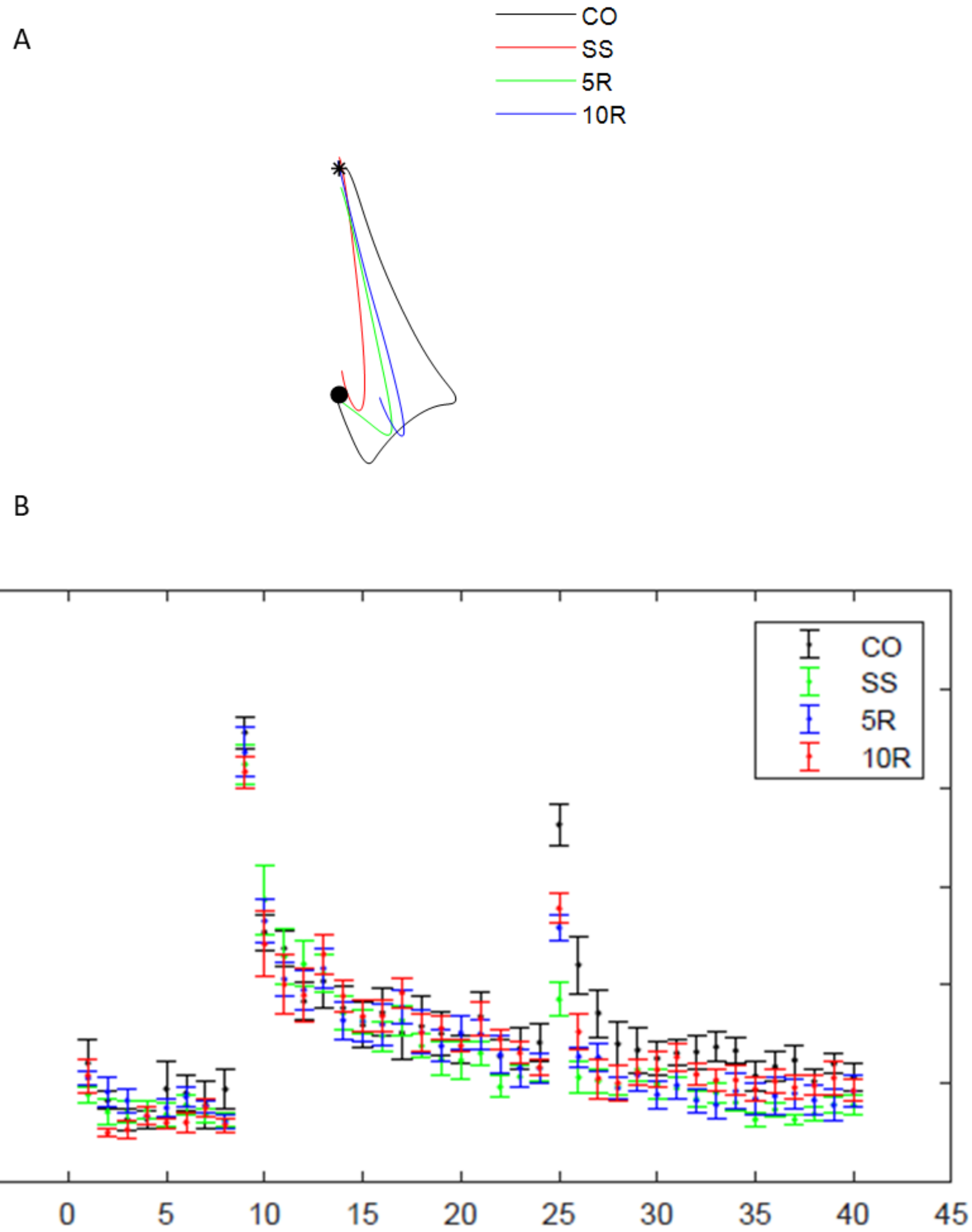

Figure 4.5: (A) Hand-paths of the subjects from the first block of the generalization session. (B) Direction errors in the baseline (Block 1-8), adaptation (Block 9-24), and transfer (Block 25-40). Every data point shown on X axis represents the mean value of one block across subjects in each group (mean ± SE).

Direction errors are shown in Figure 4.5B. A Repeated-measures ANOVA showed that the errors decreased significantly across blocks in the adaptation session (F (15,405) = 143.8, p < 0.001), and the four groups exhibited similar learning patterns, since the effect of group was not significant (F (3, 27) = 0.086, p = 0.967) and the interaction effect between group and block was not significant (F (45,405) = 1.238, p = 0.147). Another repeated-measures ANOVA revealed a significant interaction effect between group and block on the direction errors in the generalization session (F (45,405) = 4.377, p < 0.001). Post hoc analysis using the first block of the generalization session showed that subjects in the SS group exhibited smaller direction errors in the first block than subjects from the 5R and 10R groups (p < 0.004), which in turn showed smaller errors than the CO group (p < 0.001). The difference between 5R and 10R was not significant (p = 0.408).

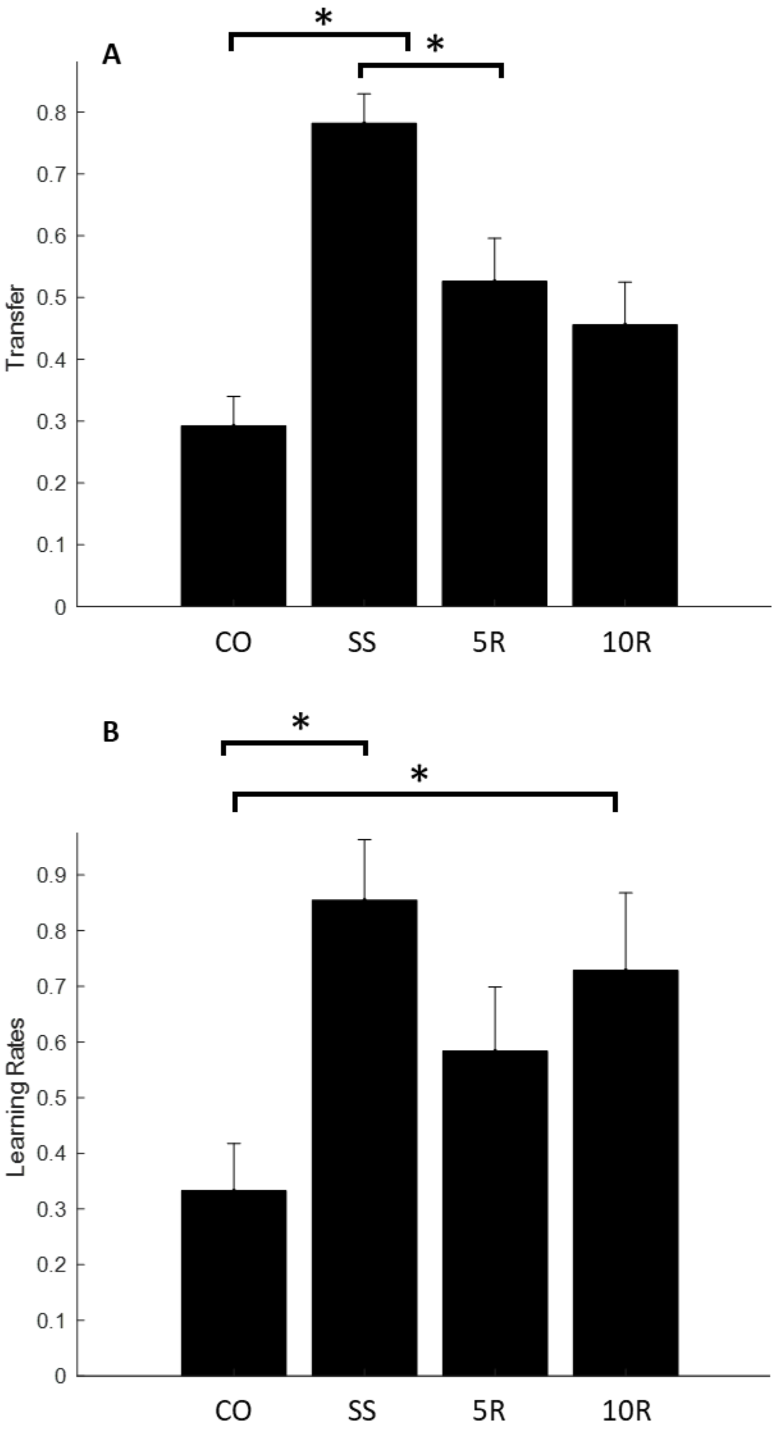

Figure 4.6: (A) Extent of transfer across directions. (B) Learning rates in the generalization session. (*p = 0.05)

The extent of transfer across directions is depicted in Figure 4.6A. The extent in the SS group was 78% ± 4% (mean ± SE), which was larger than all the other groups ($p < 0.005$). The transfer of 5R and 10R were 52% ± 6% and 46% ± 6% respectively, but the difference was not significant ($p = 0.408$). The transfer for CO group was 29.26% ± 5%, which was smaller than the 5R group ($p = 0.012$), and also tended to be smaller than the 10R group ($p = 0.070$). A one-way ANOVA showed that learning rates in the generalization session were different. The SS and 10R groups adapted to the perturbation faster than the CO group (p = 0.004 and 0.025). The 5R group also tended to show faster learning rates than CO, but did not reach the statistical significance ($p = 0.14$).

Experiment 5

In this experiment, we examined the pattern of generalization following visuomotor adaptation across movement conditions in which the direction and workspace of the movement remained the same, but the limb configuration varied.

Materials and Methods

Participants

Thirty-two subjects are recruited to this study, while the inclusion/exclusion criteria were the same as Experiment 4. According to our previous studies, the sample size was large enough to meet the most stringent statistical requirements and allowed room for possible attrition. Sixteen of the subjects had already participated in Experiment 4. Since their experimental tasks were the same, the same data were used in both Experiment 4 and 5.

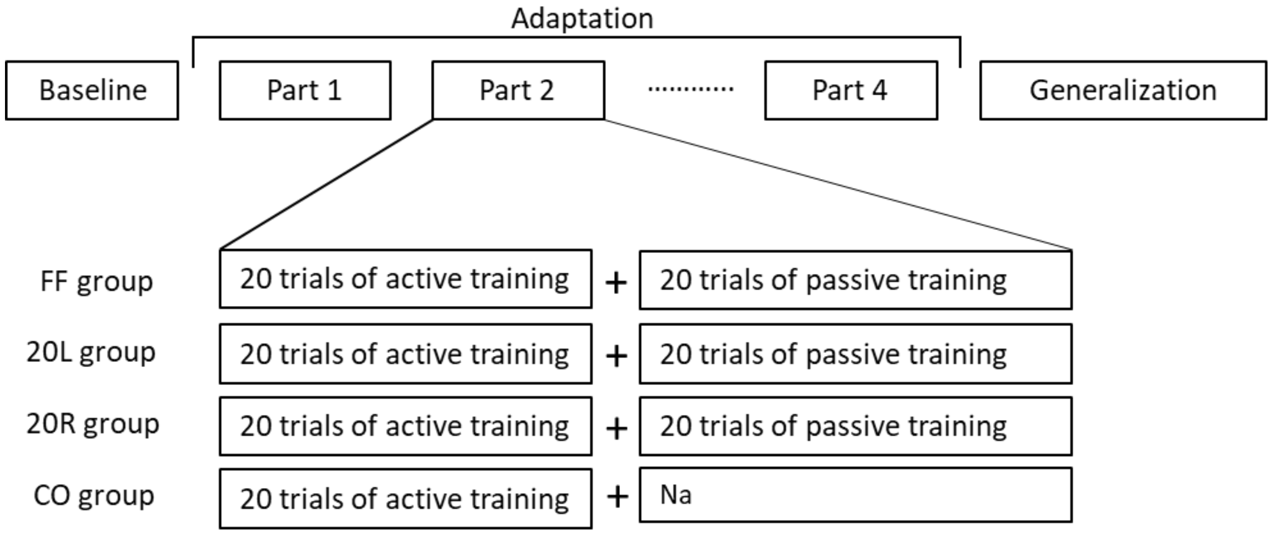

Figure 4.7: Experimental protocol for Experiment 5. The adaptation session is subdivided into four parts, and each part contains both active and passive training except for the CO group.

Apparatus

The same apparatus used in Experiment 4 was used in this part.

Experimental Protocol

The subjects were instructed to perform swift and straight target-oriented reaching movements from a start circle to one of the two targets (2 cm in diameter, 10 cm away from the start circle) that appeared to the upper (training target) or to the lower side (generalization target) of the start point as shown in Figure 4.8A. The experiment consisted of three sessions: baseline, adaptation, and generalization. Each session contained eight blocks (40 trials), 16 blocks (80 trials), and 16 blocks (80 trials) of active reaching movement, respectively (Figure 4.7). In the baseline session, the subjects reached towards the training target to get familiar with the general reaching movement. In the adaptation session, the subject adapted to a visual display that was rotated 30^o counterclockwise about the start circle. During this session, the subjects were divided into four groups: control (CO) group, forward facing (FF) group, 20-deg to the left (20L) group, and 20-deg to the right (20R) group. They all practiced to reach toward the training target, and after every four blocks (20 trials) of reaching movements, the subjects in FF, 20L and 20R groups experienced 20 extra trials of passive reaching movement which was moved by a robotic exoskeleton towards the direction that was 30^o clockwise to the generalization target, while subjects from the CO group would take a short break. Subjects in the FF group experienced passive movements with their body facing forward; those in 20L group experienced the passive movements when their trunks were rotated 20^o to the left; those in the 20R group experienced with the passive movements when their trunks were rotated 20^o to the right. During the generalization session, all subjects performed reaching movement to the generalization target with their body facing forward under a 30^o visuomotor rotation (Subjects in FF and CO groups are the same subjects in SS and CO groups in Experiment 4).

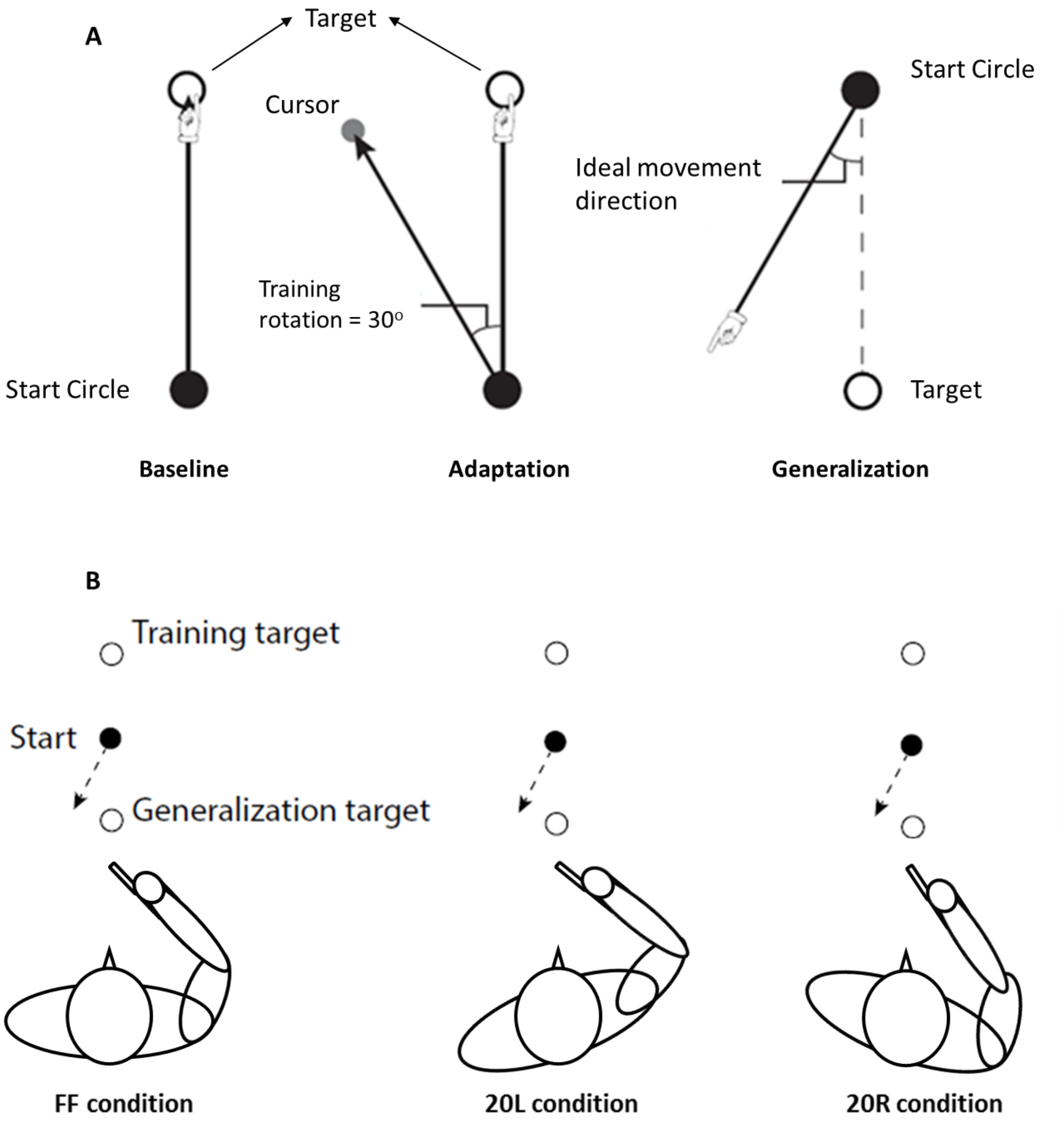

Figure 4.8: Schematic diagram of the reaching movements for Experiment 5. (A) The setup for active reaching performance. Subjects reached towards the training target in baseline and adaptation sessions, and reached toward the generalization target on the opposite side in generalization session. In adaptation and generalization sessions, the subjects needed to reach toward 30° clockwise about the target in order to make the cursor reach the target. (B) The setup for passive training. The subjects from FF group faced forward during passive trials; subjects from 20L group rotated 20° to the left; subjects from 20R group rotated 20° to the right.

Data Analysis

Direction errors from the adaptation session were subjected to a repeated-measures ANOVA with group (CO, FF, 20L, and 20R) as a between-subject factor and block as a within-subject factor to determine if there were differences among the subject groups. Another repeated-measures ANOVA with the same two factors was conducted to examine the errors from the generalization session to determine if there were differences between groups.

The learning rate in the generalization session was determined by fitting the direction error data to an exponential function. The extent of generalization across directions were calculated using the following equation: (errors of the first block in adaptation session – errors of the first block in generalization session) / (errors of the first block in adaptation session – errors of the last block in adaptation session) x 100%. Two one-way ANOVAs with group as the between subject variable were conducted: one was to compare the learning rates in the generalization session, and the other was to compare the extent of transfer across conditions.

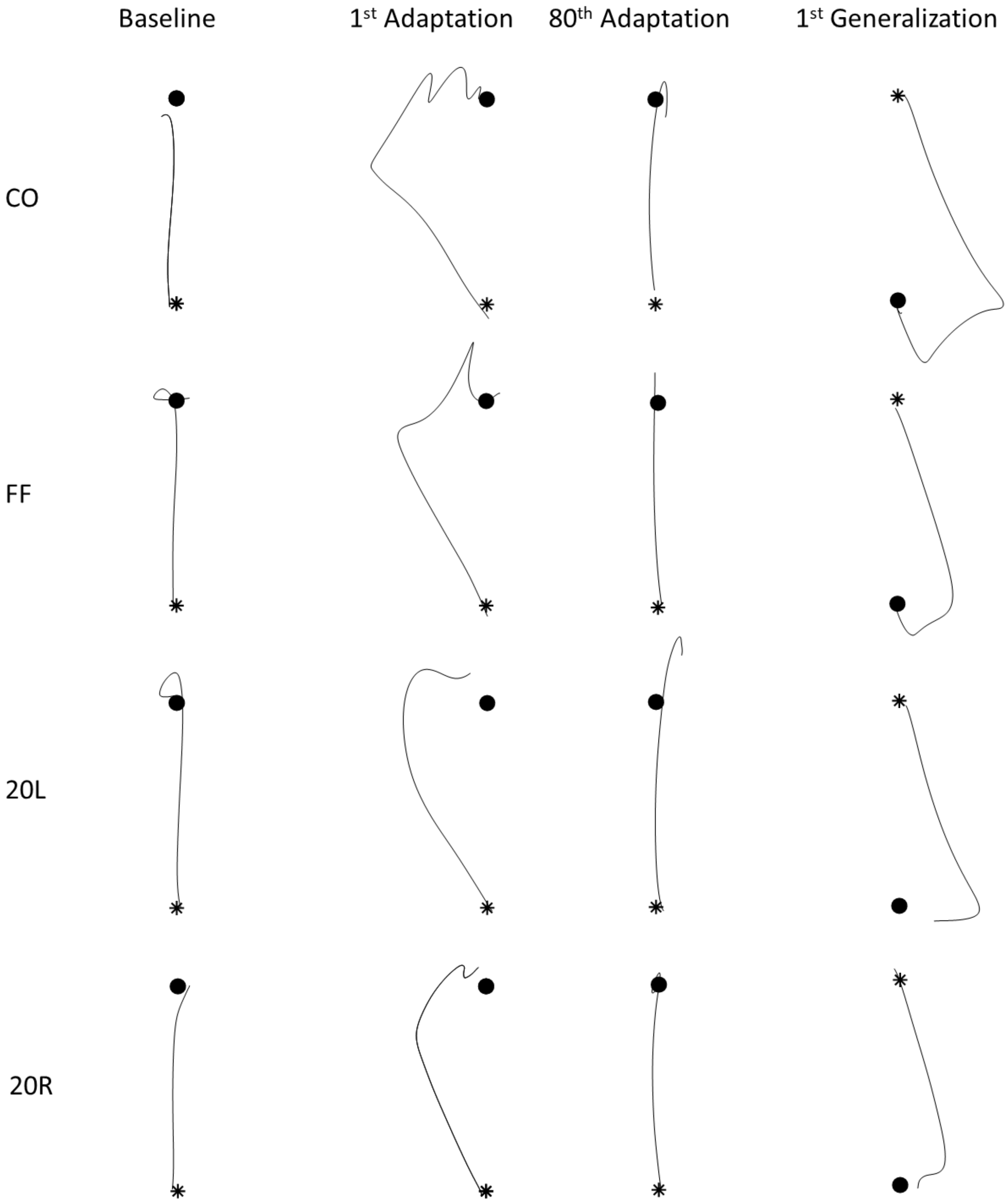

Figure 4.9: Hand-paths from representative subjects from each group (separated by row) in the baseline session (first column), first and last block of the adaptation session (second and third columns), and the first block of the generalization session (fourth column).

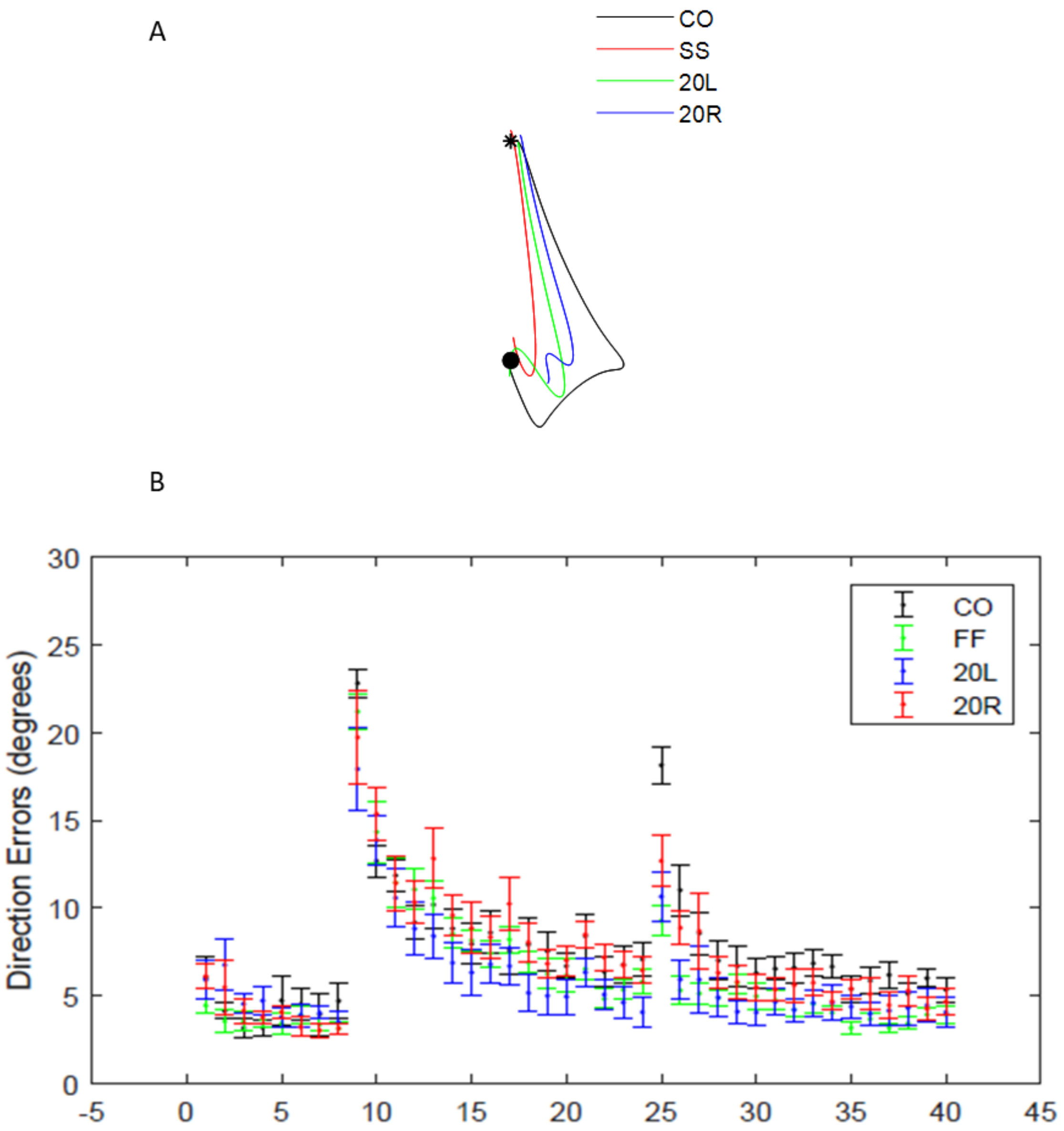

Figure 4.10: (A) Hand-paths of the subjects from the first block of the generalization session. (B)Direction errors in the baseline (Block 1-8), adaptation (Block 9-24), and generalization (Block 24-40) session. Every data point shown on X axis represents the mean value of 5 consecutive trials across subjects within each group (mean ± SE).

Results

Figure 4.9 illustrates the hand-paths of representative subjects for the baseline session, the adaptation session, and the generalization session. The hand-paths at the beginning of the adaptation session largely deviated from the target line (second column), but they became relatively straight and accurate by the end of the adaptation session (third column). The hand-paths at the first block in the generalization session were shown in the fourth column. Hand-paths shown for all four groups were largely curved again, which indicated that the generalization to the second target was incomplete for all the groups. According to Figure 4.10A, the hand-path of the subject from the CO group was more curved than those of the subjects from the FF, 20L and 20R groups who experienced reaching movements passively, indicating that the passive training benefited the subsequent performance in the same direction. The hand-path of the SS subject was relative straighter than the 20L and 20R subjects whose limb configurations were altered during the passive training.

Direction errors are shown in Figure 4.10. A Repeated-measures ANOVA showed that the errors decreased significantly across blocks in the adaptation session ($F (15,405) = 159.9$, $p < 0.001$), and the four groups exhibited similar learning patterns, since the effect of group was not significant ($F (3, 27) =1.282$, $p = 0.301$) and the interaction effect between group and block was not significant ($F (45, 405) = 1.056$, $p = 0.379$). Another repeated-measures ANOVA revealed a significant interaction effect between group and block on the direction errors in the generalization session ($F (45, 405) = 4.614$, $p < 0.001$). Post hoc analysis using the first block of the generalization session showed that subjects in CO group exhibited larger direction errors than all other groups ($p < 0.005$), indicating that subjects who experienced the passive training all exhibited substantial improvements in the generalization session. FF subjects exhibited smaller errors than 20R ($p = 0.006$), yet the difference between FF and 20L did not reach statistical significance ($p = 0.135$).

The extent of transfer across directions was depicted in Figure 4.11A. The extent of the FF group was 78% ± 4% (mean ± SE), which was larger than all the other groups ($p < 0.013$). The transfer of 20L and 20R were 55% ± 8% and 55% ± 7% respectively, while the difference between these two groups was not significant ($p = 0.989$). The transfer for the CO group was 29% ± 5%, which was smaller than all the other groups ($p < 0.009$). A one-way ANOVA revealed that the learning rates in the generalization session differed across groups ($p = 0.018$). Post hoc analysis showed that the subjects in the FF group exhibited faster learning rates than those in the CO ($p = 0.002$) and 20R ($p = 0.027$) groups. The difference between the FF and 20L groups was not different but close to reaching the statistical significance ($p = 0.059$).

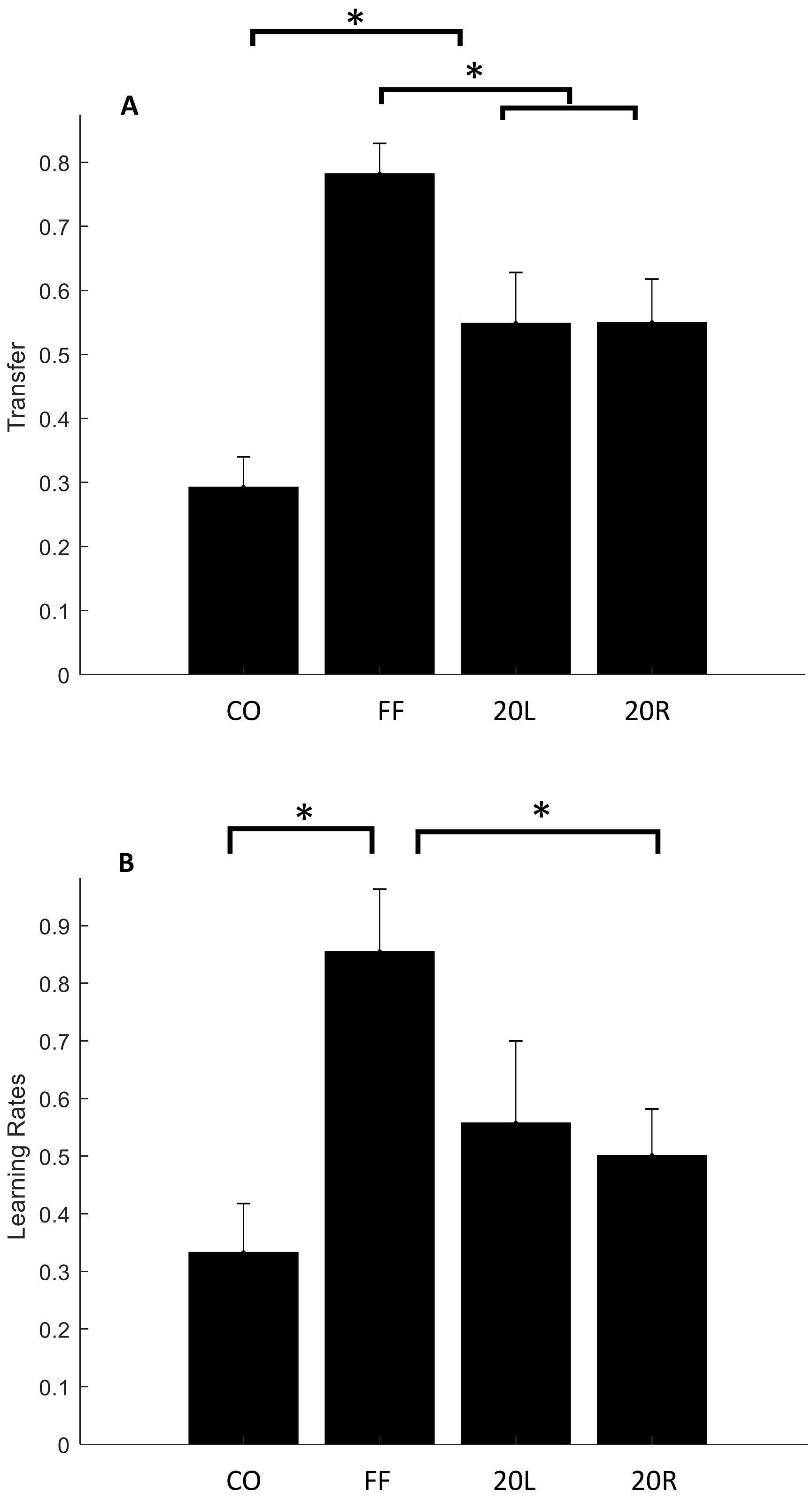

Figure 4.11: (A) Extent of transfer across directions. (B) Learning rates in the generalization session. (*$p < 0.05$)

Discussion

In this study, we aimed to investigate the nature of instance-reliant learning involved in visuomotor adaptation and its generalization. For this aim, we conducted two experiments (4 and 5) that examined the extent of transfer of visuomotor adaptation across workspace and limb configuration. In Experiment 4, we had the subjects actively practice reaching movement towards the first target, and had them accrue instances associated with the movement towards the second target without voluntarily learning it. After the training session, we examined the reaching performance towards the second target. Our data revealed that the accrued passive instances substantially reduced the direction errors from 18° to 10°, and the calculated transfer from the trained to the generalization directions increased to 78% (Figure 4.6A). This result is consistent with the finding in our previous study (Lei et al., 2017), which also demonstrated ~80% of transfer across movement directions. By shifting the workspaces of the passive training rightward, the direction errors increased approximately by 13° (5R and 10R). Though the difference between group 5R and 10R was not significant, there was a monotonic tendency in our data that the farther the workspace was shifted, the larger the errors were in the generalization session. When we shifted the workspace of passive training by 10 cm rightwards, the extent of transfer became smaller, which were not significantly different from that the CO group who did not experience any passive training (Figure 4.6A). These findings suggest that the movement specific instance can generalize across workspaces, but the generalization decays as the workspace is shifted far away from the original location.

In Experiment 5, subjects in the 20L and 20R groups experienced passive training when their trunks were rotated leftward or rightward by 20 degrees, so their limb configurations were altered during the reaching performance. They all exhibited substantial improvements compared to the CO group as the direction errors decreased by approximately 14°. However, their improvements were smaller than that of the FF group whose limb configuration was not altered (Figure 4.11A). This result shows that the generalization of instance-reliant learning decays as the limb configuration is altered as well.

By comparing the performance of the group SS and the group 5R/10R in Experiment 4, and comparing the performance of the group FF and the group 20L/20R in Experiment 5, we conclude that instance-reliant learning is workspace and limb configuration specific to a certain degree. However, subjects in the 5R/10R and 20L/20R groups did exhibit improved performance in the generalization session. The extent of normal transfer in this and our previous study (Lei et al., 2017) were both limited to be about 30%; but for those who experienced passive training, the extents of transfer were higher than 40% no matter the workspaces or limb configurations were altered. This result suggests that instance-reliant learning can still generalize across conditions, even though the training effect might decay by a substantial amount.

Instance-reliant learning in motor adaptation and generalization

As suggested by Logan (1988) and our previous studies (Wang & Sainburg, 2004, 2015), the initial phase of visuomotor adaptation is dominated by algorithmic learning, during which the CNS aligns the proprioceptive input to the visual feedback. For this learning process, the movements of end-effectors are represented in the vision-based extrinsic frame; therefore, visuomotor adaptation can generalize across spaces as long as the movement direction is the same (Ghahramani et al., 1996; Krakauer et al., 2000; Wang & Sainburg, 2005; Heuer & Hegele, 2011). However, in the late phase of adaptation, when a set of movement instances become available, retrieval of these instances competes with the algorithmic process. And by the end of the adaptation, the CNS almost completely relies on instance retrieval to achieve fast and automatized control of the performance (Wang & Sainburg, 2004, 2005). Based on the findings from this and our previous studies (Wang et al., 2015; Lei et al., 2016, 2017; Bao et al., 2017), we posit that movement specific instance is associated with both force generation and proprioceptive input. During passive training, sensory feedback from joint receptors, cutaneous receptors, and other related sensors is the only way that the movement instances can be accrued, so we consider proprioceptive input as an essential source for learning. While during active training, force generalization or the interaction between force generation and proprioceptive input should have an extra contribution to the learning, because active training usually leads to better output than passive training (Wang et al., 2015; Lei et al., 2016, 2017; Sakamoto et al., 2015).

In the discussion above, we attribute instance-reliant learning to force generation and proprioceptive input. This idea can explain why the generalization across workspace or limb configuration is incomplete: The forces/torques needed to generate the same movement output are identical, and the proprioceptive input should be consistent across trials if the limb configuration and external environment remain unchanged. So when the workspace or limb configuration is altered, the control policy associated with the original movement instance will not fit the new condition perfectly.

Instances accrued through passive training

Movement execution is a voluntary process, so it is reasonable that active training leads to instance-reliant learning. However, passive training also leads to improvement in the subsequent performance (Lei et al., 2016, 2017; Bao et al., 2017; Sakamoto et al., 2015;

Cressman et al., 2010; Diedrichsen et al., 2010), indicating that proprioceptive input must play a role during the learning, which has been discussed above. The deprivation of proprioception leads to deficiencies in motor control and motor learning. For example, Sainburg and et al. (1993) had two patients with severe large-fiber sensory neuropathies (loss of sensation) perform a gesture similar to slice a loaf of bread. Compared to the neurologically intact subjects, the patients were less able to synchronize the movements at the shoulder and elbow joints, so the output movements were curved, inaccurate, and inconsistent. The information provided by this study suggests that proprioceptive input are essential to achieve fast and automatized control of the movements.

The exact mechanism on how sensory feedback is converted into control policy remains unclear so far. One potential mechanism might be that the sensory information helps to regulate the performance. For example, the joint receptors and cutaneous receptors could provide spatial information, and the Golgi tendon organs and muscle spindles could provide dynamical information. The CNS might rely on the information to determine if the movement output is wanted and if the control policy should be refined. As mentioned above, the two patients in Sainburg's study cannot perceive the movement output, so their performance cannot be refined (Sainburg et al., 1993). During passive training, there is no need to refine the control policy; however, sensory feedback could still be stored in the CNS as a paradigm. In subsequent active performance, the CNS would try to follow the paradigm to execute the movement. This idea is compatible with the finding that passive training can bias the subsequent active performance (Sakamoto et al., 2015; Lei et al., 2016, 2017; Bao et al., 2017), even though the passive training is entirely irrelevant to the active performance (Diedrichsen et al., 2010).

Active vs. passive training

During active training, the mechanism of instance-reliant learning might differ from passive training on two main aspects. First, the efferent nerves are involved, so active training exhibits advantages in some conditions where passive training tend to be less effective. For example, during force-field adaptation, a subject is instructed to reach directly towards the target, and a velocity-dependent force pushes his arm away from desired trajectories. The subject can learn to compensate for the dynamic perturbation through active training; however, we cannot imagine how passive training could lead to adaptation in this condition.

Second, the training effect can be increased through a reinforcement process during active training (Mawase et al., 2017). This process is associated with the functions of basal ganglia (Doya, 1999, 2007; Leow et al., 2012), in which the utility of control policy is evaluated, and the CNS determines whether the current policy should be stored or forgotten (Izawa & Shadmehr, 2011; Huang et al., 2011; Leow et al., 2012). Mawase (2017) investigated the contribution of reinforcement learning to neural reorganizations of the motor cortex. He had the subjects practice sequential pinch task with the right thumb, and examined the TMS elicited actions after the training. The subjects who received a binary reward by visual feedback showed more neural reorganizations, indicating that the efficiency of instance-reliant learning was enhanced by the binary reward. This result is compatible with the findings from neuroimaging studies. The neural substrates for active and passive training are largely overlapped in cortical areas, but the activation of basal ganglia is higher during active training (Weiller et al., 1996; Ciccarelli et al., 2005). The differences in neural activations suggest that the substrates associated with the reinforcement process are more activated when the subjects voluntarily perform the movements.

Summary

In this study, the nature of instance-reliant learning is investigated. Our data shows that movement instance is workspaces and limb configurations specific because the generalizations across conditions in Experiment 4 and 5 were limited. However, subjects still exhibited substantial improvements after the passive training, no matter the workspace or limb configuration was manipulated. Since the training can generalize across workspaces, limb configurations, and magnitudes (Chapter 3), its benefit would not be restricted to the practiced skill but might have a broad impact on all the related movement skills as well.

CHAPTER 5: Summaries and Conclusions

The mechanism of motor learning and adaptation has been intensively studied in the past since it helps to explain how movement information is detected and stored in the CNS (Franklin et al., 2011; Scott, 2012; Berniker et al., 2014; Taylor et al., 2016). In our studies, we posit that the procedure of visuomotor adaptation includes two main independent processes that are algorithmic and instance-reliant learning (Wang & Sainburg, 2004; Wang et al., 2015; Lei et al., 2016, 2017; Bao et al., 2017). In this dissertation, we estimated the relative contribution of each process to visuomotor adaptation and examined the properties of the movement instance associated with the adaptation. The motivation of this study stemmed from the goal to understand the mechanisms of motor learning, and we expected that our findings would help to improve strategies for skill training and motor recoveries.

Summaries of the main findings from Experiment 1 to 5

In Experiment 1 and 2, we investigated the differential contributions of algorithmic and instance-reliant learning to the formation of visuomotor adaptation. Algorithmic learning was induced by having the subjects observe a video that another individual learned to adapt to the visuomotor rotation, and instance-reliant learning was induced by having the subject passively perform reaching movement with a robotic exoskeleton. In this way, the degrees of algorithmic and instance-reliant learning can be manipulated separately. After the observation and passive training, the learning effects were tested by having the subjects perform the same task as they observed in the video. Compared to the CO group, all the subjects who had experienced the observation and passive training exhibited substantial improvements in direction errors and learning rates in the testing session, except for the subjects in group MI, who only exhibited changes in learning rates. This result was in general compatible with the reports from previous studies that the function of active training can be partially substituted by observation and passive training (Brass et al., 2000, 2001; Heyes & Foster, 2002; Hayes et al., 2010; Mattar & Gribble, 2005; Ong & Hodges, 2010; Cressman et al., 2010; Sakamoto et al., 2015; Lei et al., 2016, 2017; Bao et al., 2017). However, the effects of these two learning processes were not exactly the same. The degree of algorithmic learning was positively associated with the direction error in the first cycle of the testing session and was also positively associated with the learning rate in the following cycles. By contrast, instance-reliant learning only influenced the direction error of the testing session, while the learning rates were not different across the three groups (FI, PI, and MI).

In Experiment 3 ~ 5, we investigated the nature of instance-reliant learning associated with visuomotor adaptation. In Experiment 3, we examined whether the adaptation could generalize across conditions in which the movement magnitudes varied. We found that the generalization from large to small magnitudes was complete, but the generalization from small to large was incomplete (~50%), indicating that the direction of the PR reaching was not directly assigned to FR reaching in which the magnitude was ten times larger. In Experiment 4 and 5, we examined whether the movement instance was workspace and limb configuration specific. We had the subjects actively practice reaching movement towards the first target and had them accrue instances associated with the movement towards the second target through passive training. Then we examined the performance towards the second target to determine if the preceding passive training would benefit the reaching movement in the same direction. According to the results, passive training did improve the subsequent performance by reducing the direction errors by at least 5 degrees, which was compatible with our previous study (Lei et al., 2016, 2017; Bao et al., 2017). However, the generalization across workspaces or limb configurations was not complete, since by shifting the workspace of the passive training rightward, or by rotating the trunk of the subject left or rightward, the improvements declined significantly. Combining the findings from Experiment 3 to 5, we conclude that movement instance is magnitude, workspace, and limb configuration specific to a certain degree.

Mechanism of visuomotor adaptation and its generalization across various conditions

The transfer of motor learning across limbs, directions, and postures has been studied widely in the past, not only because it has practical importance for rehabilitation techniques, but also because it provides substantial insights into the mechanism underlying skill acquisition (Wang et al., 2015; Poh et al., 2016). So far, the exact mechanism of visuomotor adaptation is still under debate; however, most of the recent studies suggest that adaptation involves at least two learning processes: a fast process which is sensitive to the feedback errors, and a slow process which is less sensitive to the sensory feedback but is in charge of skill consolidation (Wang & Sainburg et al., 2004, 2015; Smith et al., 2006; Huang et al., 2011; Bond & Taylor, 2015; Poh et al., 2016; Lei et al., 2016, 2017; Bao et al., 2017). In our previous studies, we have suggested that those two processes coincide with algorithmic learning and instance-reliant learning based on our investigation on intralimb and interlimb transfer of visuomotor adaptation (Wang & Sainburg, 2004; Wang et al., 2015; Lei et al., 2017).

In this study, we find that movement instance is magnitude, workspace, and limb-configuration specific. According to previous studies, instance-reliant learning is also effector specific and direction specific, since the transfer of visuomotor adaptation is usually limited to about 30% (Wang & Sainburg et al., 2004; Lei et al., 2011; Wang et al., 2015; Poh et al., 2016; Carroll et al., 2014; Balitsky et al., 2010). So based on these facts, instance-reliant learning is movement specific in general. In the next session, we will talk about how to maximize the learning effect based on our findings of instance-reliant learning.

Algorithmic learning is another important mechanism in visuomotor adaptation. As introduced in Chapter 1, it is also termed error-based learning or model-based learning (Huang et al., 2011; Diedrichsen et al., 2010). In conventional opinion, it refers to an implicit process that the visuomotor relationship is remapped in a step-by-step manner (Miall & Wolpert, 1996; Kawato, 1999; Mazzoni & Krakauer, 2006); however, in recent studies, it is also suggested to be an explicit learning process (Taylor & Ivry, 2014; McDougle et al., 2015; Poh et al., 2016), or a mix of explicit and implicit processes (Taylor et al., 2011; Huberdeau et al., 2015; Haith et al., 2015). As discussed in Chapter 4, algorithmic learning is represented in the vision-based Cartesian coordinate, so it can generalize across limb configuration and workspaces as long as the movement direction is the same (Ghahramani et al., 1996; Krakauer et al., 2000; Wang & Sainburg, 2005). Some researchers suggest that the visuomotor maps for different end-effects are partially overlapped (Wang et al., 2004; Balitsky et al., 2010; Carroll et al., 2014) so that the extent of transfer across limbs are not zero.

Instance-reliant learning in rehabilitation techniques and robot-assisted therapy

Instance-reliant learning might be the most common way to acquire new skills and is considered as the theoretical basis of rehabilitation training for patients with post-stroke hemiparesis (Butefisch et al., 2000; Kent et al., 2008; Kreisel et al., 2006; Maher et al., 2006). As mentioned in Chapter 1, instance-reliant learning is usually termed use-dependent learning, practice-dependent learning, experience-dependent changes, or use-dependent plasticity in the literature (Butefisch et al., 2000; Karni et al., 1998; Kent et al., 2008; Kreisel et al., 2006). The ultimate purpose of rehabilitation training is not only to regain some specific skills but also to broadly restore motor and sensory functions to achieve qualified daily lives. Therefore, rehabilitation programs rely heavily on the assumption that learning in one context can generalize to another context, so patients do not need to practice all the movements for daily activities. Fortunately, movement specific instances can generalize across multiple conditions, which means that standardized physiotherapies could benefit multiple daily activities. Moreover, the performance trained in simplified conditions also benefits other performances in complicated situations. For example, to restore walking abilities after stroke, the training strategy does not need to be a walking practice if it is too challenging for the patient. By contrast, it could be a series of simplified movements such as trunk stability, step initiation, and weight support on the paretic leg and these skills will generalize across conditions (e.g., weight, posture, environment) and benefit the walking performance in the long run (Schwartz, et al., 2009).

If the ultimate purpose is to acquire a specific skill, we will not like the inefficiency due to the generalization across conditions such as magnitudes, postures, and so force. By contrast, we will attempt to practice the skill directly and efficiently. For example, in order to play the piano, a player needs to increase flexibility, dexterity, and strength of his fingers. Even though he could improve his fingers by practicing plucking the guitar strings, he will not do it, since the most efficient way to achieve his goal is to practice the piano directly. For stroke patients, however, it might be too challenging for them to prefer the efficient training. For example, as mentioned in the last paragraph, if the patient cannot practice walking at all, the therapist can provide some other alternative training that is relevant to walking. Based on the discussion above, we know that rehabilitation training might be less effective because the movement instances accrued through conventional hand-to-hand physiotherapy do not perfectly match the requirement for daily activities.

One method to increase the efficiency of instance-reliant learning is to introduce robotic-assisted training to conventional physiotherapy. There are two prominent advantages of robotics. First, they enable the stroke patient to practice the specific skill which is needed (Conroy et al., 2011; Pohl et al., 2007), so the movement instances can directly benefit the actual performance (Kitago et al., 2015; Schwartz et al., 2009). Second, with the support of robotics, patients can practice movements with wider ranges. In this way, learning can generalize from more experienced movements/conditions/contexts to the unexperienced ones, which means that the benefit of training is not only the specific skills but also some unpracticed skills through generalization. A large number of studies have shown that robotic-assisted therapy generates better results in motor recoveries than conventional hand-to-hand physiotherapy (Chang & Kim, 2013; Schwartz et al., 2009; Kitago et al., 2015; Fasoli et al., 2004; Hsieh et al., 2012), which is consistent with our expectation. As an example, Schwartz (2009) compared the outcomes of gait training between two groups of patients. One of the groups only received conventional hand-to-hand physiotherapy, and the other group received both robotic-assisted therapy and conventional hand-physiotherapy as well. The robotic-assisted therapy involves different kinds of gait practice under the help of a robotic-driven orthosis (Lokomat, Hocoma Inc., Zurich, Switzerland). After the six weeks of treatment, patients all exhibited improvements in walking abilities and neurological status, but the patients from the robotic therapy group exhibited more improvements in gait velocity, endurance, and stairs climbing.

Comparing instance-reliant learning and reinforcement learning

In our studies, instance-reliant learning is considered as the process that visuomotor adaptation is consolidated (Wang & Sainburg, 2004; Wang et al., 2015; Lei et al., 2017). However, in some articles, researchers posit that consolidation is accomplished through reinforcement learning (Huang et al., 2011; Kitago et al., 2013; Haith & Krakauer, 2013). Reinforcement learning, or termed model-free learning, refers to the mechanism that the CNS evaluates the movement output and determines whether the current commands should be reinforced or erased (Doya, 1999, 2007; Leow et al., 2012; Izawa & Shadmehr, 2011). Based on its definition, the concept of reinforcement learning is partially overlapped with that of instance-reliant learning. The difference is that reinforcement learning emphasizes that only the useful instances are stored in the CNS, but instance-reliant learning suggests that all the instances are stored no matter they are useful or useless (Mawase et al., 2017; Diedrichsen et al., 2010; Verstynen & Sabes. 2011).

The role of reinforcement learning in visuomotor adaptation has been investigated in previous studies (Huang et al., 2011; Wang et al., 2015). As similar to instance-reliant learning, it is effector specific (Wang et al., 2015), and direction specific (Huang et al., 2011). However, it exhibits different characteristics in visuomotor adaptation. According to Huang’s study (Huang et al., 2011) and our Experiment 2, instance-reliant learning does not influence the learning rate; however, reinforcement learning could affect the learning rate substantially (Huang et al., 2011).

As mentioned in Chapter 4, Mawase et al. (2017) investigated the interaction between instance-reliant learning and reinforcement learning, finding that by providing a binary reward to the movement instance, the output of instance-reliant learning is improved by a large scale. This finding leads to the question: Is reinforcement learning a specific form of instance-reliant learning? Since their concepts are similar in general, while the distinction of reinforcement learning is that, the movement instances are evaluated, filtered, and reinforced (or erased) before they are stored.

Future design for passive instance-reliant training

In the discussion above, we know that observation and passive training are not sufficient to achieve complete visuomotor adaptation. Compared to our previous study (Lei et al., 2017), the numbers of training trials are increased; however, the improvements are not apparent, indicating that there is an upper limit for the protocols used for our experiments. In Chapter 2, we attribute this limitation to two factors: (a) subjects have less chance to correct errors in control policy (Beets et al., 2012), since the error detection/correction loops are not activated enough; (b) neural activations tend to be lower during passive training (Weiller et al., 1996; Ciccarelli et al., 2005), which indicates that the CNS is less devoted to the task. Based on these two points, the effect of passive training might be augmented in two ways below.

The first method is to make the brain more “devoted” to motor learning. During active training, feedback of successful performance works as a reward for the control policy (Doya, 1999, 2007; Izawa & Shadmehr, 2011; Mawase et al., 2017). Here, we present a protocol aiming to enhance the reinforcement process during passive training. As shown in Figure 5.1A, normal and perturbed reaching are provided to the subjects in pseudorandom orders. For perturbed reaching, the arm does not reach towards the correct direction, and negative reward will be provided when the performance is finished (e.g., the word “Failure” is displayed on the screen). For normal reaching, the arm reaches along the direction of the solid line arrow, and positive reward will be provided (e.g., the word “Success” is displayed). We expect that binary reward will facilitate the use-dependent plasticity, resulting in more improvements in the subsequent performance (Mawase et al., 2017; Kooij et al., 2018). According to the report by Kooij (2018), abundant reward might have a negative effect on the outputs, because reinforcement learning competes with other learning processes. So in the schematic diagram, as shown in Figure 5.1B, we suggest that reward is provided to only 25% of the trials, while half is positive reward, and half is negative reward.

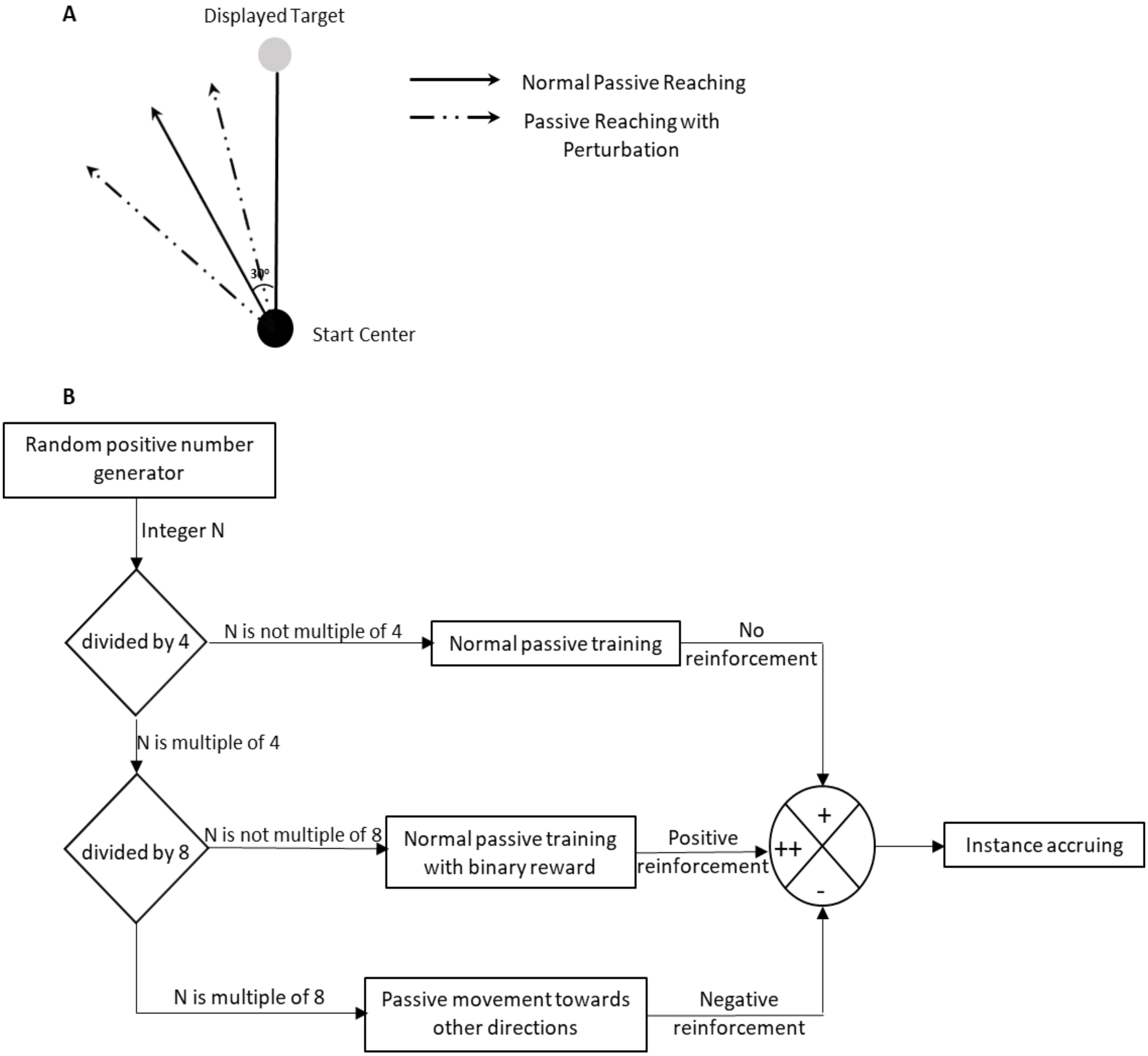

Figure 5.1: Schematic diagram that binary reward is involved during passive training. (A) The setup for passive reaching and randomized perturbations. (B) Binary reward is provided to part of the reaching trials. As shown in the flow chart, 25% of the trials receive reward. Half of them are positive reward, and half are negative reward.

Another method is to induce visuospatial remapping during passive training (Figure 5.2). For our passive training, visual feedback was removed in order to inhibit the process of visuospatial remapping (top panel of Figure 5.2). However, in the literature, such as Cressman's (2010) and Sakamato's (2012, 2015) studies, the outcomes of passive training are better when visual feedback is provided. The reason might be that algorithmic learning and instance-reliant learning are both ongoing. Therefore, if we want to increase the outcomes of passive training, we can try to provide visual feedback, as shown in the bottom panel of Figure 5.2.

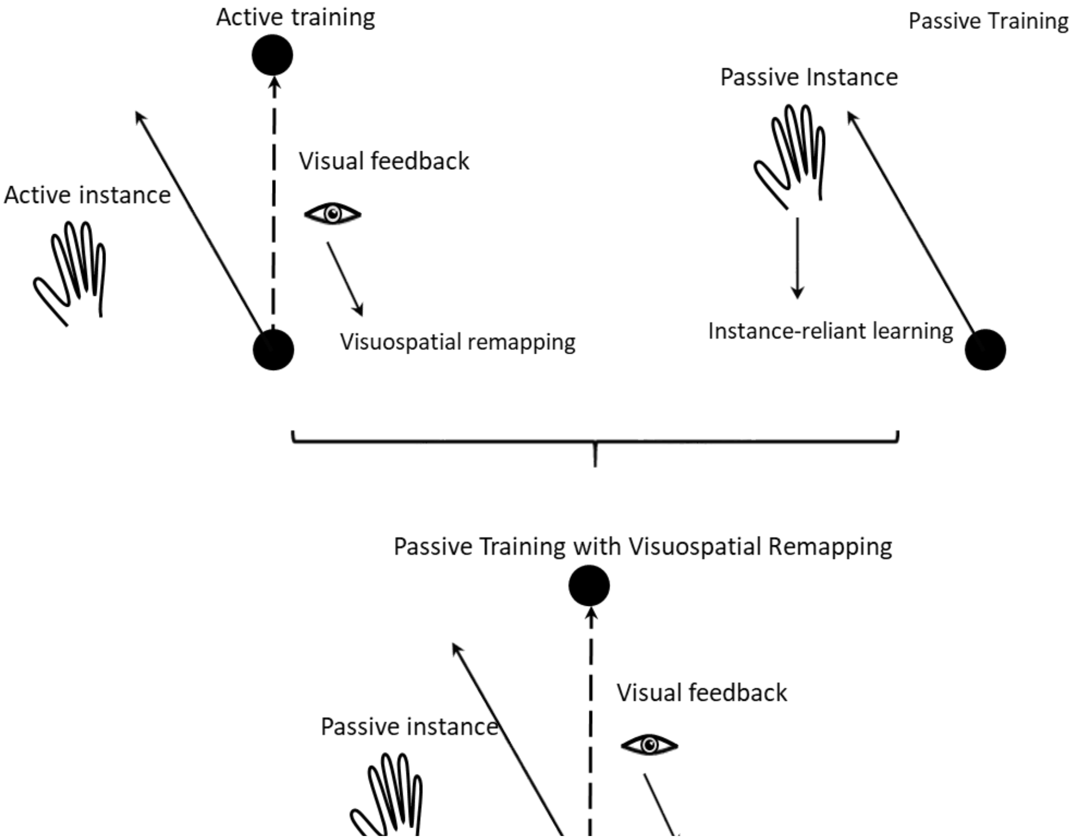

Figure 5.2: Schematic diagram of visuospatial remapping during active and passive training.

Figure 5.3: Schematic diagram that binary reward is involved during passive training. (A) The setup for passive reaching and randomized perturbations. (B) Binary reward is provided to part of the reaching trials. As shown in the flow chart, 25% of the trials receive reward. Half of them are positive reward, and half are negative reward.Figure 5.4: Schematic diagram of visuospatial remapping during active and passive training.

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APPENDIX A: Informed Consent Form

UNIVERSITY OF WISCONSIN – MILWAUKEE
CONSENT TO PARTICIPATE IN RESEARCH

THIS CONSENT FORM HAS BEEN APPROVED BY THE IRB FOR A ONE YEAR PERIOD

1. General Information

Study title: Investigating the contribution of instance-reliant learning in visuomotor adaptation and its generalization.

Person in Charge of Study (Principal Investigator):

My name is Dr. Jinsung Wang. I am an associate professor in the Department of Kinesiology at University of Wisconsin -- Milwaukee. The study described below will be conducted by Mr. Shancheng Bao, who is the Student Principal Investigator (SPI).

2. Study Description

You are being asked to participate in a research study. Your participation is completely voluntary. You do not have to participate if you do not want to.

Study description:

The purpose of this study is to investigate the role of passive movements in visuomotor adaptation and its generalization. Passive movement training is one of intervention techniques used in clinical rehabilitation for persons with arm movement impairment, such as stroke patients. However, the mechanisms that underlie the benefits of this type of training is not well understood. In this research study, we are trying to compare a passive movement training condition to other similar training conditions, which should help us understand the mechanisms underlying passive movement training better, so that we can find a way to maximize its beneficial effects.

This study will be conducted in the Neuromechanics Laboratories at UWM. Approximately 128 volunteers will participate in this study. Your participation in this study will take approximately one hour and half, over the course of one day.

Eligibility:

If you are a healthy individual, defined as a person who does not have any neurological damage, and are right handed and aged between 18 and 35, you are eligible to participate in this study. You will be excluded for following criteria: 1) a major psychiatric diagnosis (e.g., schizophrenia), 2) hospital admission for substance abuse, 3) peripheral disorders affecting sensation or movement of your arms (e.g., peripheral neuropathy), or 4) if you are left-handed.

3. Study Procedures

What will I be asked to do if I participate in the study?

If you agree to participate you will be asked to come to the Neuromechanics Laboratories, located on the first floor of Enderis Hall at UWM. Upon your arrival, an experimenter will first have you fill out a handedness questionnaire, which comprises a set of questions to determine which hand you use to perform given activities (e.g., which hand to hold a broom), and then describe the task to you. After that, you will sit at a table, and a computer game will be projected on a computer display in front of you. Though you may not see your hand, you will see the position of your hand as a cursor, projected on the screen. You will be asked to position this cursor in a start circle located in the middle of the screen. At computer-generated tones, you will be asked to move your hand toward targets presented on the screen. You may be asked to use your right arm, left arm, or both at the same time, depending on the condition you are assigned to. It will take approximately one and a half hours for you to complete an experiment.

Your arm movements will be recorded using a non-invasive, 2-dimensional robotic system where you will rest your arms on robotic armrests. No audio/video/photographic recordings will be made.

4. Risks and Minimizing Risks

What risks will I face by participating in this study?

This research involves minimal risk, that is, no risks to physical or mental health beyond those encountered in the normal course of everyday life. During the experiment, however, some minor discomfort associated with remaining seated for over an hour may be experienced. When that happens, you may request a break to stretch and rest your arms, although you will have to remain seated in the KINARM chair until the end of the experiment because removing yourself from that chair will require recalibration of the system.

5. Benefits

Will I receive any benefit from my participation in this study?

Participation in this research has no direct benefit you, beyond that of financial reimbursement, and the opportunity to participate in research that may prove valuable for the development of more efficient rehabilitation protocols for stroke patients.

Are subjects paid or given anything for being in the study?

In return for their participation, you will be asked to choose to receive $10 in cash or class extra credit. If at any time you discontinue participation in the study, you will receive $5 in cash. Class extra credit will be offered to students of the PI (1% point out of 100% point scale toward the final grade) or those instructors who encourage their students to participate in any faculty research and offer an extra credit for doing that (please ask the instructor regarding the amount of credit). If you prefer receiving cash, you will need to provide personal information (Name, DOB, SSN, contact information), by filling out the payment/credit information form and also the payment record sheet.

6. Study Costs

Will I be charged anything for participating in this study?

You will not be responsible for any of the costs from taking part in this research study.

7. Confidentiality

What happens to the information collected?

All information collected about you during the course of this study will be kept confidential to the extent permitted by law. We may decide to present what we find to others, or publish our results in scientific journals or at scientific conferences. Information that identifies you personally will not be released without your written permission. Only the PI, and other personnel assigned by the PI, will have access to the information. However, the Institutional Review Board at UW-Milwaukee or appropriate federal agencies like the Office for Human Research Protections may review your records.

The only records that maintain your identity will be this consent form and the questionnaire; both this form and the questionnaire will be kept locked in the PI's laboratory. The collected data will be saved with your initial (e.g., jw for Jinsung Wang) as part of the data file name (e.g., jw0001). This is necessary to process and analyze the data from each participant separately. These data cannot be associated with you without access to your consent form that is kept locked in the PI's laboratory. Only the PI and specific personnel assigned by the PI will have access. After the study is complete, the data will be kept in the PI's password-protected computer for up to six years; it will be destroyed afterwards.

8. Alternatives

Are there alternatives to participating in the study?

If you are currently a student of the PI, you may choose to complete an extra reading assignment (i.e., to read a research article determined by the PI and to submit a one-page written critique to the SPI), which requires approximately the same time to complete it; and the same extra credit will be given for that assignment. You are not allowed to participate in this study AND complete the reading assignment.

9. Voluntary Participation and Withdrawal

What happens if I decide not to be in this study?

Your participation in this study is entirely voluntary. You may choose not to take part in this study. If you decide to take part, you can change your mind later and withdraw from the study. You are free to not answer any questions or withdraw at any time. Your decision will not change any present or future relationships with the University of Wisconsin Milwaukee. And we will destroy all information we collect about you.

10. Questions

Who do I contact for questions about this study?

For more information about the study or the study procedures or treatments, or to withdraw from the study, contact:

Dr. Jinsung Wang
Department of Kinesiology
College of Health Sciences
University of Wisconsin -- Milwaukee
492 Enderis Hall
Milwaukee, WI, 53201
(414) 229-3226

Who do I contact for questions about my rights or complaints towards my treatment as a research subject?

The Institutional Review Board may ask your name, but all complaints are kept in confidence.

Institutional Review Board
Human Research Protection Program
Department of University Safety and Assurances
University of Wisconsin – Milwaukee
P.O. Box 413
Milwaukee, WI 53201
(414) 229-3173

11. Signatures

Research Subject's Consent to Participate in Research:

To voluntarily agree to take part in this study, you must sign on the line below. If you choose to take part in this study, you may withdraw at any time. You are not giving up any of your legal rights by signing this form. Your signature below indicates that you have read or had read to you this entire consent form, including the risks and benefits, and have had all of your questions answered, and that you are 18 years of age or older.

____

Printed Name of Subject/ Legally Authorized Representative

____ ____________________

Signature of Subject/Legally Authorized Representative Date

Principal Investigator (or Designee)

I have given this research subject information on the study that is accurate and sufficient for the subject to fully understand the nature, risks and benefits of the study.

____ ____________________

Printed Name of Person Obtaining Consent Study Role

____ ____________________

Signature of Person Obtaining Consent Date

APPENDIX B: Handedness Questionnaire

Handedness Questionnaire

Name: Age:

Height: Weight:

This questionnaire is designed to thoroughly evaluate one's degree of handedness. Please place a check mark in the appropriate box for each task. If you use both hands, check both, but indicate the one used more often or that you feel is more controlled. If you have any questions, do not hesitate to ask.

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

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, please explain ____

4. Is there any activity not in this list that you do consistently with your Left Hand?

If yes, please explain ____

APPENDIX C: Recruitment Flyer

Subjects Needed

The Neuromechanics Laboratory is seeking subjects for research to study the motor learning mechanisms underlying passive training.

Subjects must be **18 to 35 years of age** and must be **right hand** dominant.

As a subject, your arm movements will be recorded while you play a computer game. The entire procedure is non-invasive and comfortable. The session will last for approximately one hour and a half.

You may receive monetary compensation or extra credit (please confirm with your course instructor(s)) for participating in this research. An alternative assignment (i.e., reading a research article and writing a one-page critique) is also available for same extra credit.

Please send me an email at **sbao@uwm.edu**

for more information about this study or the alternative assignment, or to schedule a time.

APPENDIX D: Curriculum Vitae

Education

Ph.D. (exp.)	Department of Kinesiology, University of Wisconsin- Milwaukee (UWM)	Dec 2019
MS	Department of Biomedical Engineering, Marquette University (MU)	May 2013
BE	Department of Biomedical Engineering, University of Electronic Science and Technology of China (UESTC)	Jun 2008

Research Experience

Aug. 2013 – Now	Doctoral study in neuromotor control/learning Department of Kinesiology, University of Wisconsin-Milwaukee Advisor: Dr. Jinsung Wang
Jul. 2010 – May. 2013	Research project: “Supra-Spinal Contributions to Upper and Lower Limb Motor Control and Recovery after Stroke --- An fMRI Study.” Advisor: Dr. Sheila Schindler-Ivens, Dr. Michelle Johnson, and Dr. Jinsung Wang
Jan. 2010 – Dec. 2011	Research Assistant in Rehabilitation Robotic Research Design Lab in Clement J. Zablocki Department of Veterans Affairs Medical Center, Milwaukee, WI Advisor: Dr. Michelle Jillian Johnson
Oct. 2007 – Jun. 2008	Senior Design: “Stimulus Design for Event-related Potential” in UESTC Advisor: Dr. Dezhong Yao
Dec. 2006 – Mar. 2007	Undergraduate Assistant in the ElectroencePhalography Lab in UESTC; Advisor: Dr. Xiaoli Liao

Teaching Experience

Mar 2019	Guest lecture in Analytical Methods in Engineering (ELECENG 150): A Guided Tour of Magnetic Resonance Imaging
Sep 2018 – Dec 2018	Course assistant in Physical Rehabilitation and Performance Psychology Course: Gross Anatomical Kinesiology (PRPP 725, 3 credits)
Jun 2015 – Aug 2018	Teaching assistant in Kinesiology Course 1: Motor development across lifespan (KIN 460, 3 credits) Course 2: Principle of motor learning (KIN 461, 3 credits) Course 3: Introduction to Kinesiology (KIN 200, 3 credits)
May 2016– Aug 2016	Guided teaching experience in Health Science (KIN 460, 3 credits) (developed the course material for 'Motor development across lifespan (KIN 460, 3 credits)' and taught it as the main instructor under the supervision of Dr. Jinsung Wang)
Jun 2015 – Aug 2018	Teaching assistant in Kinesiology Course 1: Motor development across lifespan (KIN 460, 3 credits) Course 2: Principle of motor learning (KIN 461, 3 credits) Course 3: Introduction to Kinesiology (KIN 200, 3 credits)

Publications

Bao, **S**., Lei, Y., & Wang, J. (2017) Experiencing a reaching task passively with one arm while adapting to a visuomotor rotation with the other can lead to substantial transfer of motor learning across the arms. *Neuroscience Letters*, *638*, 109-113.

Wang, J., **Bao, S.**, Tays, G. (Accepted) Lack of generalization between explicit and implicit visuomotor learning. *PLOS One*.

Lei, Y., **Bao**, **S**., Perez, M. A., & Wang, J. (2017) Enhancing Generalization of Visuomotor Adaptation by Inducing Use-dependent Learning. *Neuroscience*, *366*, 184-195.

Lei, Y., **Bao**, **S**., & Wang, J. (2016) The combined effects of action observation and passive proprioceptive training on adaptive motor learning. *Neuroscience*, *331*, 91-98.

Conference Abstracts/Posters

Bao, **S**., Morgan, A., Lei, Y., & Wang, J. (2018) Lack of interlimb transfer following visuomotor adaptation in a person with congenital mirror movements. Program No. 492.08. Neuroscience Meeting Planner. San Diego, CA: Society for Neuroscience, 2018. Online

Bao, **S**., Tays, G., & Wang, J. (2017) The extent of overlap between explicit and implicit visuomotor learning. Program No. 694.13. Neuroscience Meeting Planner. Washington, DC: Society for Neuroscience, 2017. Online

Bao, **S**., Lei, Y., & Wang, J. (2016) Augmenting motor generalization by inducing instance-reliant plasticity. Program No. 332.11. Neuroscience Meeting Planner. San Diego, CA: Society for Neuroscience, 2016. Online

Bao, **S**., & Wang, J. (2015) Persistence of a neural representation following repeated adaptations to and repeated deadaptations from a novel visuomotor rotation. Program No. 806.21. Neuroscience Meeting Planner. Chicago, IL: Society for Neuroscience, 2015. Online

Manuscripts in Preparation

Bao, **S**., Morgan, A., Lei, Y., & Wang, J. (Review) Lack of interlimb transfer following visuomotor adaptation in a person with congenital mirror movements.

Bao, **S**., D'Amato, A., James, R., & Wang, J. (Data available) Visuomotor adaptation and deadaptation with one arm results in saving during subsequent visuomotor adaptation with the other arm.

Bao, **S**., & Wang, J. (Data available) Contribution of algorithmic learning and instance-reliant learning to visuomotor adaptation.

Bao, S., & Wang, J. (Data available) Instance-reliant learning is influenced by movement magnitudes.

Bao, **S**., & Wang, J. (Data available) Instance-reliant learning is influenced by workspace and limb-configuration.

Tays, G., **Bao, S.**, Javidialsaadi, M., Wang, J. (Data available) Consolidation of use-dependent motor memories induced by passive proprioceptive training.

Research Skills

Movement data acquisition using KINARM (BKIN Technologies, Ontario, Kingston, Canada).

TMS/EMG data acquisition using Magstim 200^2 (Magstim Co Ltd, Spring Gardens, Whitland, UK) and MR3 (Noraxon, Scottsdale, AZ).

Computer programming and data acquisition using Presentation (Neurobehavioral Systems Inc, Albany, CA).

Computer programming using MATLAB/GUI (MathWorks, Natick, MA).

FMRI data analyzing (fMRI) using AFNI (open source, mainly developed by Medical College of Wisconsin, Milwaukee, WI).