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Shancheng Bao
Texas A&M University
jinsung Wang
University of Wisconsin–Milwaukee
David Wright
Texas A&M University
John Buchanan
Texas A&M University
Yuming Lei (yxl907@tamu.edu)
Texas A&M University

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The Decay and Consolidation of Effector-Independent Motor Memories

Shancheng Bao[1], Jinsung Wang[2], David L. Wright[1], John J. Buchanan[1], and Yuming Lei[1]

1. Department of Health and Kinesiology, Texas A&M University, College Station, TX, 77843.
2. Department of Kinesiology, University of Wisconsin-Milwaukee, Milwaukee, WI 53151.

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Correspondence to:
Yuming Lei, PhD.
Department of Health and Kinesiology
Texas A&M University
Phone: (979) 862–3392
E-mail: yxl907@tamu.edu

Abstract

Learning a motor adaptation task produces intrinsically unstable or transient motor memories. Despite the presence of effector-independent motor memories following the learning of novel environmental dynamics, it remains largely unknown how those memory traces decay in different contexts and whether an “offline” consolidation period protects memories against decay. Here, we exploit inter-effector transfer to address these questions. We found that newly-acquired motor memories formed with one effector could be partially retrieved by the untrained effector to enhance its performance when the decay occurred with the passage of time or “washout” trials on which error feedback was provided. The decay of motor memories was slower following “error-free” trials, on which errors were artificially clamped to zero or removed, compared with “washout” trials. However, effector-independent memory components were abolished following movements made in the absence of performance error, resulting in no transfer gains. The brain can consolidate motor memories during daytime wakefulness. We found that 6 hours of wakeful resting increased the resistance of effector-independent memories to decay across all contexts. Collectively, our results suggest that the decay of effector-independent motor memories is context dependent and offline processing preserves those memories against decay, leading to improvements of the subsequent inter-effector transfer.

Introduction

Inter-effector transfer of motor learning refers to a process whereby initial training with one effector leads to subsequent performance gains with the opposite untrained effector. Substantial evidence has demonstrated the presence of inter-effector transfer of learning across multiple motor tasks in humans[1-6] and non-human primates[7-9], and indicated that neural networks subserving effector-independent motor memories provide the gateway for such transfer[10-13]. For example, neuroimaging and behavioral studies revealed that the parietal cortex and its connectivity with the motor and visual regions are engaged during inter-effector transfer[12] and the inhibition of the left posterior parietal cortex blocks the transfer[14]. Electrophysiological studies using paired-pulse brain stimulation indicated that interhemispheric plasticity mediates inter-effector transfer[10,15]. Elucidating the mechanisms underlying inter-effector transfer of motor learning not only provides substantial insights into neural communications between the hemispheres but also has important implications for clinical rehabilitation, sports, and tool use. For example, human lesion studies showed that initial training with the non-paretic effector is beneficial to motor skill acquisition of the paretic effector in stroke patients[16,17]. Resistance training with one effector results in strength gains in the untrained effector[3,18]. Non-human primate studies showed that learning a tool-use task over two weeks with one effector increases performance gains in the opposite effector[8].

Motor adaptation tasks, such as adapting to visuomotor or mechanical perturbations during reaching movements, are widely used to study our ability to apply what has been learned with one effector to the other[1,2,19]. Generally, motor adaptation produces memories that are fragile and susceptible to interference[20-22], which can later be forgotten through

distinct decaying processes: (1) one process whereby motor memories are actively disengaged when the brain detects changes in context[22-24], and (2) one process in which the decay is a form of memory forgetting due to an intrinsic feature of error-based learning[25-27]. If the decay of motor memories is supported by two different processes, how are the effector-independent memory components affected by these processes? Do these decaying processes make different contributions to the patterns of inter-effector transfer? Importantly, can effector-independent memories be consolidated against these processes?

Here, we employed a series of experimental methods to examine the decay of effector-independent motor memories engaged in different contexts and probed their influences on the resultant inter-effector transfer. We hypothesized that distinct decaying processes with one effector would result in different gains for subsequent performances with the untrained effector. Research has shown that the brain can consolidate motor memories during wakefulness[28,29]. For example, neuroimaging[30] and electrophysiological[31] studies showed that offline consolidation of a motor memory could occur over the hours following its formation, which is associated with changes in brain plasticity[32]. Behavioral studies showed that offline processing during wakefulness is prominent as evidenced by the increased resistance of the memory to interference[29,33,34]. Notably, previous studies of motor adaptation indicated that 6-hour of wakeful resting is a critical amount of time necessary for offline consolidation[35,36]. Therefore, we hypothesized that a 6-hour window of offline processing would preserve effector-independent motor memories against decaying processes.

Results

Experiment 1: Effector-independent memories can be retrieved when the decay occurs with the passage of time or "washout" trials. During the learning session, all subjects made point-to-point movements with their left arm under conditions in which visual feedback was rotated 30^o CCW (Figure 1A). Figure 1B, C (left) depict changes in direction error (DE) across trials during the learning session for each group. As expected, the DEs were large due to the exposure to the novel visuomotor rotation, which decreased progressively throughout the session. Repeated-measures ANOVA showed an effect of TRIAL ($F_{(2, 36)} = 346.1$, $p < 0.001$), but not GROUP ($F_{(1, 18)} = 0.055$, $p = 0.8$), or their interaction ($F_{(2, 36)} = 0.867$, $p = 0.4$) on DE. During the decaying session, Group1.1 experienced 200 "washout" trials. The DEs were returned to the baseline state by removing the visual rotation and providing error signals (asymptotic DE = 4.1±1.6^o, baseline DE = 5.0±2.2^o, p=0.6; Figure 1B, middle). Group1.2 sat idle for 840 s, which was the average amount of time taken by subjects in Group1.1 to complete 200 trials (Figure 1C, middle). Figure 1B, C (right) shows changes in DE across trials during the transfer session in Group1.1 and Group1.2 compared with a naïve control group who experienced the visual perturbation with the right arm for the first time. Repeated-measures ANOVA showed an effect of TRIAL ($F_{(2, 54)} = 359.0$, $p < 0.001$), GROUP ($F_{(2, 27)} = 20.0$, $p < 0.001$), and their interaction ($F_{(4, 54)} = 25.5$, $p < 0.001$) on DE. This indicated that the changes in motor performance across trials were different among the three groups. Figure 2A illustrates the representative cursor-paths of a representative subject from Group1.1 and Group1.2 during the first trial of the learning and transfer session and from the control group during the first trial of the learning session. The cursor-paths (gray

lines) all deviated largely from the target direction, indicating that the subjects were unable to compensate for the visual perturbation at the beginning of the learning session. The cursor-path (black line) during the transfer session from Goup1.1 was also largely biased towards the CCW direction, which indicated that the subjects in this group could not accurately move the cursor to the target during the initial period of inter-effector transfer. However, the cursor-path (black line) of the Goupr1.2 was more accurate compared with the control group (broken line), revealing that the adapted behavior could be retrieved by the untrained effector at the first trial of the transfer session. In agreement, Group data showed that DEs from the first trial during the transfer session were smaller in Group1.2 (18.4±4.0^{o}; Figure 2B) compared with Group1.1 (31.9±4.1^{o}, $p<0.001$) and the control group (32.8±5.2^{o}, $p<0.001$). No difference was found between Group1.1 and the control group ($p=0.6$). The percentage of initial transfer observed in Group1.2 (55±25%) was significantly higher than that observed in Group1.1 (-6±34%, $p<0.001$). The learning rate of errors was higher in Group1.1 (0.58±0.4; Figure 2C) compared with Group1.2 (0.15±0.15, $p=0.01$) and the control group (0.16±0.08, $p=0.02$), whereas no difference was observed between Group1.2 and the control group ($p=0.9$). This indicated that the prior motor memories could be accessed by the untrained arm in the form of savings (faster relearning) when decaying occurred with “washout” trials on which the rotation was removed, and error signals were provided. In the control experiment, the subjects sat idle for 3 min during the decaying session, neither the extent of initial transfer nor learning rate was different between those subjects and Group1.2 in which the subjects sat idle for about 15 min.

Experiment 2: Effector-independent memories are abolished when the decay occurs in the absence of errors. Motor adaptation is driven not only by sensory prediction errors (discrepancies between predicted and actual sensory consequences[37]), but also by task errors (discrepancies between predicted and actual task outcomes[38]). Motor memories are actively disengaged in the absence of those errors that drive adaptation[22,25]. In Experiment 2, we examined the decay of effector-independent memories in the absence of errors using three different types of error-free trials. Figure 3A-C (left) depict changes in DE across trials during the learning session for three groups. Repeated-measures ANOVA showed an effect of TRIAL ($F_{(2, 54)}$ = 486.6, $p < 0.001$), but not GROUP ($F_{(2, 27)} = 0.193$, $p = 0.8$), or their interaction ($F_{(4, 54)} = 0.123$, $p = 0.9$) on DE. The DEs returned back toward baseline during the decaying sessions in Group2.1 (asymptotic DE = 6.1±2.1°, baseline DE = 5.2±2.6°, p=0.4; Figure 3A, middle) and Group2.3 (asymptotic DE = 7.1±1.8°, baseline DE = 5.5±2.6°, p=0.3; Figure 3C, middle). The DEs were set to be zero due to the force-clamp during the decaying session in Group2.2 (Figure 3B, middle). Notably, the decay rates were slower during error-free trials on which error signals were clamped to zero (Group2.1=0.10 ± 0.08, p=0.01) or removed (Group2.3=0.15 ± 0.13, p=0.03) compared with "washout" trials (Group1.1=0.46 ± 0.36). Although the rate of decaying appeared faster in Group2.3 compared with Group2.1, this difference was not statistically significant (p=0.3). Following the error-free trials, all subjects were re-exposed to the same perturbation for 80 trials with the opposite, untrained arm. Repeated-measures ANOVA showed an effect of TRIAL ($F_{(2, 72)} = 552.0$, $p < 0.001$), but not GROUP ($F_{(3, 36)} = 1.959$, $p = 0.2$), or their interaction ($F_{(6, 72)} = 0.63$, $p = 0.7$) on DE during the transfer session (Figure 3A-C, right). The

lack of difference was further confirmed by calculating DEs at trial 1 during the transfer session, as well as the learning rate of the untrained effector. Figure 4A-C (left) show the representative movement trajectories of a representative subject from three error-free groups (colored line) and the control group (black line) upon initial exposure to the rotation during the transfer session. The trajectories were similarly deviated across all these subjects. DEs at trial 1 during the transfer session were not significantly different among the four groups (GROUP [$F_{(3, 36)}$ = 0.813, p =0.5]; Figure 4A-C, middle). The ANOVA across the four groups using the learning rates showed no effect of GROUP ($F_{(3, 36)}$ = 1.381, p =0.3; Figure 4A-C, right) either, indicating no savings following either error-clamp or no-error feedback trials. Overall, these results suggest that the effector-independent memories cannot be retrieved by the untrained effector when the decay of memories occurs in the absence of errors.

Experiment 3: Offline processing consolidates effector-independent motor memories. We next examined whether offline processing could consolidate effector-independent motor memories. Motor memories formed during adaptation can be enhanced over wakefulness[30,39]. Do effector-independent motor memories benefit from offline consolidation? To test that, we replicated the design of Experiment 1 and 2, except that participants underwent the learning session in the morning and experienced the transfer session 6 hours later without any intervening sleep. Because we found no difference among the groups throughout the learning and transfer sessions in Experiment 2, we only replicated Group2.1 in which the subjects experienced visual error-clamp trials during the decaying session. Figure 5A-C (left) illustrate

the performance during the learning session for each group. Repeated-measures ANOVA showed an effect of TRIAL ($F_{(2, 54)} = 511.5$, $p < 0.001$), but not GROUP ($F_{(2, 27)} = 0.63$, $p = 0.5$), or their interaction ($F_{(4, 54)} = 0.032$, $p = 0.9$) on DE. Following 6 hours of wakeful resting, the subjects were randomly assigned to one of three groups to participate in the decaying session. Group3.1 and Group 3.2 experienced 200 "washout" trials and error-clamp trials, respectively (Figure 5A-B, middle). The DEs were returned to baseline in both groups (Group3.1: asymptotic DE = 3.7±0.9°, baseline DE = 4.9±1.4°, p=0.2; Group3.2: asymptotic DE = 7.1±1.9°, baseline DE = 5.3±2.2°, p=0.1). Group3.1 exhibited smaller DEs by the end of the decaying session compared with Group3.2 ($p<0.01$). The subjects in Group3.3 sat idle for 860 s, which was the average amount of time taken by the subjects in Group3.1 and Group3.2 to complete the decaying session. During the transfer session, effector-independent motor memories were present in the form of savings in all three group (Figure 5A-C, right). We found an effect of TRIAL ($F_{(2, 72)} = 483.9$, $p < 0.001$) and GROUP ($F_{(3, 36)} = 7.411$, $p = 0.001$), but not their interaction ($F_{(6, 72)} = 1.68$, $p = 0.1$) on DE. The one-way ANOVA showed an effect of GROUP ($F_{(3, 36)} = 3.61$, $p = 0.02$; Figure 6A-C, right) on learning rate. *Post hoc* analysis showed that learning rates increased significantly in all three experimental groups compared with the control group (Group3.1=0.56±0.46, p=0.02; Group3.2=0.67±0.50, p=0.01; Group3.3=0.57±0.47, p=0.02; Control group=0.16±0.08). Movement trajectories observed at trial 1 of the untrained effector was less deviated from the target line in Group3.3 (Figure 6C, left), whereas movement trajectories were noticeably more curved in Group3.1 and Group3.2 (Figure 6A-B, left). In agreement, average DEs from trial 1 during the transfer session were smaller in Group3.3 (27.6±3.1°, p=0.01; Figure 6C, middle)

compared with the control group (32.8±5.2^{o}). No difference was found between the other two groups (Group3.1=31.6±7.1^{o}, p=0.7; Group3.2=30.6±6.8^{o}, p=0.4) and the control group (Figure 6A-B, middle). Hence, 6-hour offline consolidation was sufficient to protect effector-independent memories against decay across all movement contexts, even tested in the absence of errors.

Discussion

In the present study, we provide clear evidence that the decay of effector-independent motor memories is highly context dependent. Specifically, effector-independent motor memories can be recalled by the untrained effector when motor memory decay occurs with the passage of time or at "washout" trials on which movements are made in the same context as the baseline. The retrieval of effector-independent memories is blocked if the decay occurs when the brain detects context changes from error-clamp trials and no-error trials. The brain can actively enhance motor memories during daytime wakefulness or sleep[40-42]. We further suggest that 6 hours of wakeful resting following motor memory formation protects latent motor effector-independent memories, manifest as savings, against decay across all contexts, resulting in improvements of inter-effector transfer.

The decay of effector-independent motor memories. Motor adaptation with one effector develops motor memories that comprise effector-independent components, which can subsequently be accessed by its counterpart[1,43,44]. However, those memories formed during the adaptation are inherently transient[20-22], and can be forgotten or unlearned immediately and automatically[24]. Here, we demonstrated that the manner in which the decay of motor memories occurs with one effector has significant consequences for the subsequent performance with the other effector. We found substantial initial transfer from the trained to the untrained effector when the decay occurred with the passage of time, indicating that effector-independent motor memories did not decay away following a short period of inactivity and were still available to benefit subsequent performances of the untrained effector. These

data are congruent with previous findings showing that individuals can recall the motor memory of adapted behavior after an idle period[24,45-47]. Notably, we found that the 15-min resting period does not cause larger decaying of effector-independent memories compared with 3-min rest. This agrees with studies showing that a resting period for minutes does not lead to unlearning of motor memories[46,48]. When motor memory decay occurred at "washout" trials, latent motor memories formed during adaptation, manifest as savings, were executed with the untrained effector. Evidence showed that motor memory formation during adaptation is attributed to distinct learning processes: error-driven update of internal models[49,50], operant processes and strategic selection of actions[51,52,53,54]. We suggested that internal memory models of the novel sensorimotor conditions were unlearned following the "washout" trials. This is supported by our results that the errors returned to baseline during the decaying session, and that the errors in the first trial of the transfer session were similar to those in the first trial in the control group. However, latent motor memories formed through operant processes or strategic solutions were preserved because the brain detected no novel contexts during the "washout" trials; instead, the brain just switched between the perturbation context and the baseline context. During the transfer session, the brain seems to use the first trial to probe whether the latent memories formed with the trained effector was useful for subsequent performances with the untrained effector[43,55,56]. If the latent motor memories were determined useful after the first trial, the nervous system would utilize them to facilitate subsequence performances, thus resulting in savings.

In Experiment 2, we found the lack of initial transfer and savings when motor memory decay occurred during error-free trials on which errors were artificially clamped to zero (Visual-

and Force-Clamp) or removed (No Feedback), indicating that the motor memories developed through motor adaptation were completely erased following these three conditions and could not be retrieved by the untrained effector. These results suggested that motor memories were actively disengaged when the brain detected changes in contexts. Indeed, the subjects were requested to perform movements in new or unfamiliar contexts (i.e., reaching without visual feedback, reaching in the error clamp), which they have not experienced previously (or would not perform in typical contexts). In this case, the motor memories associated with the novel visuomotor rotation (from the learning session) and the motor memories associated with the new contexts (from the decaying session) would compete for the same neural resources, especially given that the same motor effector was used in both sessions. In consequence, the prior motor memories would be actively disengaged and overwritten by the newly formed motor memories. This argument is in agreement with the previous findings that multiple motor memories stored in the brain can compete with each other for retrieval[45,55-58]. Our findings are also consistent with the findings reported by Kitago[24] that savings was not observed within the same arm following 200 error-clamp trials and no-feedback trials.

The consolidation of effector-independent motor memories. When errors were absent during the decaying session, effector-independent motor memories were completely abolished. We argued that motor memories, which did not have enough time to be consolidated yet, were disengaged if the brain actively engaged in a new movement context. If true, then offline consolidation occurring over a period of time should be sufficient for preserving those memories against decay and interference. We tested this in Experiment 3 by providing a 6-hour window of wakeful resting between the learning and decaying sessions. Previous studies of

motor adaptation have shown that a 6-hour period is a critical amount of time necessary for offline consolidation[35,36], and sleep does not add any additional benefits to offline processing[30,36,39,59]. In agreement, our previous studies showed that motor memory stabilization occurred over the 6-hour window[34]. In Experiment 3, we found that prior motor memories could be accessed by the untrained effector in the form of savings in all three groups, suggesting that a 6-hour period of wakeful resting following initial learning might consolidate motor memories developed through operant processes. Notably, we found that the errors in the first trial of the transfer session increased in Group3.3 who sat idle for 15 min following 6-hour window (27.6±3.1^{o}) compared with Group1.2 who sat idle for about 15 min without 6-hour window (18.4±4.0^{o}). This indicates that the 6-hour period of wakeful resting bore no effects on the memory consolidation process of error-based learning. The result is also supported by the reduced aftereffects in the first trial of the decaying session in Experiment 3 compared with Experiments 1 and 2. Our findings are consistent with the idea that motor memory formation during operant processes[60,61] and offline improvements developed during wakefulness[62,63] are regulated by the primary motor cortex (M1). We argue that operant learning itself increases M1 excitability and this increase leads to offline consolidation of operant processes.

Functional considerations. A critical question that we attempted to address in the current study was how distinct decaying mechanisms would mediate the nature of effector-independent motor memories associated with motor adaptation and whether effector-independent memories could be consolidated against these decaying processes. Here, we demonstrated that context-dependent decay is a feature of effector-independent motor

memories and those memories can be enhanced by offline consolidation. Our finding has an important implication for movement rehabilitation for neurological disorders or musculoskeletal injuries. For example, initial training with the non-paretic hand can lead to subsequent performance gains in the paretic hand in stroke patients[16]. As our finding indicates, however, the beneficial effect of the non-paretic hand training in rehabilitation could be eliminated if newly-acquired motor memories formed with non-paretic hand are engaged in different contexts without memory consolidation. Some strategies might be available to minimize such decaying effects. For example, exercise[64,65] and non-invasive motor cortex stimulation[57,66-68] can cause motor memories to be consolidated faster. Whether and how such methodologies can minimize the effect of distinct decaying environments (thus to maximize the effect of non-paretic side training) remains to be investigated.

Materials and Methods

Subjects

Ninety-eight healthy right-handed individuals (18-35 years old, 56 females) with no history of neurological or musculoskeletal disorder participated in this study. All subjects were naïve to our apparatus, the paradigm, and the purpose of the study. All experimental protocols were approved by the Institutional Review Board of Texas A&M University. All subjects gave written informed consent prior to participation, which was approved by the local ethics committee at Texas A&M University in accordance with the Declaration of Helsinki.

Apparatus

A bilateral robotic exoskeleton KINARM (BKIN Technologies Ltd, Kingston, ON, Canada) was used to collect movement data. The subjects were seated on the height-adjustable chair with both arms supported horizontally by the KINAM exoskeleton. The linkages of the exoskeleton were adjusted to custom-fit each subject according to their arm length and geometry. The KINARM was incorporated with a virtual reality system that projected visual targets on a horizontal display to make them appear in the same plane as the arm. The chair was moved to bring the arms under a horizontal display. Direct vision of the arm was blocked; a white cursor representing the location of index fingertip was provided to guide the subject's reaching movement. The 2-D position of the index fingertip was sampled at 1000 Hz, low-pass filtered at 15 Hz, and differentiated to yield resultant movement velocity. Data were processed and analyzed offline using MATLAB (Mathworks, Natick, MA).

Experimental design

The general motor task was to control the white cursor to perform reaching movements from a start circle to a target circle (1 cm in radius white circles, 10 cm apart). The target circle was located in the 45^{o} direction from the start circle. The subjects first moved their index finger (cursor) to the start circle, and stopped there. A trial was initiated and the start circle turned green when the cursor remained within the start circle at a speed <0.1 cm/s. Then, the subjects were instructed to move the cursor from the start circle to the target rapidly and accurately once the target appeared. Movements were required to have a reaction time (RT) of < 600 ms and a movement time (MT) within 400-800 ms. If RT > 600 ms, no visual feedback regarding movement trajectory was available and the trial was aborted. The color of the target turned red or blue if the movement was too fast (MT < 400 ms) or too slow (MT > 800 ms), and such trials were aborted as well. The target color turned green when the performance met the MT requirement (400 ms < MT < 800 ms).

Our aims were (1) to understand the decay of effector-independent motor memories engaged in different contexts, and (2) to probe their influences on a resultant inter-effector transfer task. In a series of tasks, we varied contexts and examined how those memory traces decayed across contexts (Experiment 1 and 2). This was followed up with another series of tasks (Experiment 3) in which the hypothesis that offline consolidation preserves effector-independent memories against decay across all contexts was tested. Three groups (n=30) of subjects participated in Experiment 1. Group1.1 (n=10) and Group1.2 (n=10) experienced four sessions (Figure 1A): baseline, learning, decaying, and transfer. In the baseline session, the subjects repeated the reaching movements for 80 trials (40 trials with each arm,

counterbalanced) with veridical visual feedback to be familiarized with the general motor task. In the learning session, all subjects adapted with the left arm to a visual display that was rotated 30^{o} counterclockwise (CCW) about the start circle for 80 trials. In the decaying session, Group1.1 experienced 200 "washout" trials with the left arm on which the visual perturbation was removed, and error feedback was provided throughout the entire reaching movement in each trial. Group 1.2 sat idle for about 15 min, which was around the same amount of time that Group1.1 spent to complete the decaying session. Group1.1 and Group1.2 were re-exposed to the same visual perturbation to perform reaching movements with the right arm for 80 trials in the transfer session. A group of subjects (n=10) only experienced baseline (40 trials with each arm, counterbalanced) and learning (80 trials with right arm) sessions. This control group served as our benchmark for right arm learning performance without any transfer gains from learning with the left arm. To assess the effect of time on the decay of effector-independent memory, we performed a control experiment (n=8). The subjects underwent the baseline and learning session, exactly as Group1.2. However, they continued the transfer session after sitting idle for only 3 min.

Motor memories are thought to be actively disengaged due to the absence of errors that drive adaptation[22,25]. In Experiment 2, we used different types of error-free trials to examine the potential effect of context on the decay of effector-independent memories. Three groups (n=30) of subjects participated in Experiment 2. All groups experienced four sessions, in which the baseline, learning, and transfer sessions were identical to the reaching task in Group1.1. In the decaying session, Group2.1 (n=10) experienced 200 visual error-clamp trials in which the visual feedback of movement trajectory was clamped to a straight line between the

start and target circle and thus spatially independent of actual performance. Group2.2 (n=10) experienced 200 force-clamp trials in which the subjects moved in a force channel, bounding the straight-line path between the start and target circle by generating reactive forces with a stiffness of 1500 N/m and damping of 5 N/m/s[69]. The channel was implemented as in the equation below:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} -1061 & -1061 \\ -1061 & -1061 \end{bmatrix} \begin{bmatrix} X \\ Y \end{bmatrix} + \begin{bmatrix} -3.54 & 0 \\ 0 & -3.54 \end{bmatrix} \begin{bmatrix} V_x + V_y \\ V_x + V_y \end{bmatrix} + \text{THETA} \quad (N)$$

$$\text{THETA} = \begin{cases} \begin{bmatrix} 37 \\ 37 \end{bmatrix}, & X + Y > 0.0354 \\ \begin{bmatrix} 1061 & 1061 \\ 1061 & 1061 \end{bmatrix} \begin{bmatrix} X \\ Y \end{bmatrix}, & |X + Y| \leq 0.0354 \\ \begin{bmatrix} -37 \\ -37 \end{bmatrix}, & X + Y < -0.0354 \end{cases}$$

where F_x and F_y (N) were forces applied along the medial-lateral and anterior-posterior directions, X and Y (m) were the spatial positions obtained by the relative displacement from the start circle, V_x and V_y (m/s) were the x and y components of the end-point velocity. A velocity-dependent viscous force was added to maintain stability in the direction that was perpendicular to the channel. Note that sensory prediction error was clamped to zero in the visual- and force-clamp trials. Group2.3 experienced 200 trials with no visual feedback of performance errors.

Offline processing transforms a newly acquired motor memory from a fragile state to a stable state[30,34,42,70]. In Experiment 3, we examined the effect of 6 hours of wakeful resting between the learning and decaying session on the consolidation of effector-independent motor memories. Three groups (n=30) of subjects participated in Experiment 3. All subjects experienced baseline and learning sessions in the morning. After 6 hours, the subjects were randomly assigned to three experimental groups to participate in the decaying session. For

Group3.1, the decaying session had 200 “washout” trials. For Group3.2, the decaying session had 200 error-clamp trials. Subjects in Group 3.3 sat idle for about 15 min, which was the same amount of time that Group3.1 and Group3.2 spent to complete the decaying session. Following the decaying session, all subjects were exposed to the same visual perturbation with the untrained effector for 80 trials.

Data Analysis

To examine performance accuracy, we calculated direction error (DE), which was the angular difference between a vector from the start circle to the target and another vector from the hand position at movement start to that at peak arm velocity. To assess the extent of inter-effector transfer, we compared the DE of the first trial in the transfer session to that observed on the first naïve learning trial in the control group who learned with the right arm without any transfer gains from learning with left arm. Smaller DE at trial 1 in the transfer session would indicate generalization from the left arm to the right arm. DE at trial 1 was used because subsequent trials in the transfer session were not a “pure” measure of generalization, confounded by the learning with the untrained effector. The percentage of initial inter-effector transfer was also calculated using a “within-subject” measurement using the following formula: [(left arm DE at trial 1 of the learning session – right arm DE at trial 1 of the transfer session) / (left arm DE at trial 1 of the learning session-left arm asymptotic DE of the learning session)]*100 (%). The asymptotic DE represents the mean of the last 20 trials of the learning session with the left arm. In addition, we also calculated the learning rate to determine if the rate of motor adaptation with the right arm following initial training with the left arm was

different across the groups. The learning rate was obtained by fitting with a single decaying exponential function for each subject based on the following equation: Errors (n) = A * exp (- R * n) + B. R was the individual learning rate, A and B were two constants, and n was the trial index. All statistical analyses were conducted using MATLAB and SPSS (version 27; IBM). Normal distribution was tested by the Shapiro-Wilk's test and homogeneity of variances by the Levene's test of equality and Mauchly's test of sphericity. When normal distribution could not be assumed, data were log transformed. When sphericity could not be assumed, the Greenhouse-Geisser correction statistic was used. Repeated measures ANOVAs were performed to determine the effect of GROUP and TRIAL [initial bias (trial 1), early learning (mean of trial 2-10), and asymptote learning (mean of trial 61-80)] on DE. One-way ANOVAs and independent t-tests were conducted to determine if the extent of inter-effector transfer and the learning rate were different across the groups in each experiment. Tukey post hoc analysis was used to test for significant comparisons. Alpha value was set at 0.05. Group data were presented as mean ± standard error.

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Figure legends

Figure 1. Protocols and the motor performance for Experiment 1. **(A)** The experimental protocol consisted of four sessions: baseline (veridical feedback), learning (30^o CCW rotation), decaying, and transfer (30^o CCW rotation with the opposite arm). The cursor feedback was CCW rotated by 30^o from the hand-path in the learning and transfer sessions. **(B)** Mean time-course of the movement errors of the learning, decaying, and transfer sessions were plotted in red lines across trials for Group 1.1. Standard errors were represented as the shaded area plot. Veridical cursor feedback was provided during the decaying session as shown in the mid panel. The control group's right arm performance in the transfer session was plotted as black line in the right panel for comparison. **(C)** Mean time-course of the movement errors for Group 1.2 in blue lines. The subjects sit idle during the decaying session (mid panel). The control group's right arm performance was plotted in black in the right panel for comparison.

Figure 2. (A) Hand-paths from representative subjects observed on the first trials during the learning (gray) session and transfer (black) sessions for Group 1.1 (left) and 1.2 (right). The hand-path for the control group was plotted in dashed line. **(B)** Mean errors of the first trial in the transfer session for Group 1.1 (red), 1.2 (blue), and control (black) (mean ± standard error). **(C)** Comparison of learning rates in the transfer session for the control and Group 1.1 and 1.2. *$p < 0.05$.

Figure 3. Performance for Experiment 2. **(A)** The movement errors of Group 2.1 in the learning, decaying, and transfer sessions were plotted in green lines and shaded areas (mean ± standard error). During the Decaying session, the cursor feedback was always on the straight line connecting the start and target circles. The black plot represented the control group's

performance in the transfer session. The performance of Group 2.2 and 2.3 were depicted in **(B)** and **(C)**, respectively. During the decaying session, a force channel restricted the hand-paths of Group 2.2 along the straight line connecting the start and target circles, so the hand-paths were always straight and accurate. No cursor feedback was provided for Group 2.3 during the decaying session, so the subjects reached towards the target based on their proprioception.

Figure 4. Hand-paths from representative subjects observed on the first trials during the transfer session were compared between the experimental groups (color) and the control (black) in the left panels for 2.1, 2.2, and 2.3, respectively (**A-C**, left). Mean errors of the first trial were plotted (mean ± standard error) in the mid panels (**A-C**, middle), and the learning rates were plotted on the right panels (**A-C**, right). N.S. indicates not significant ($p > 0.05$).

Figure 5. Performance of Experiment 3. **(A)** The movement errors of Group 3.1 in the learning, decaying, and transfer sessions were plotted in red lines and shaded areas (mean ± standard error). The decaying session was 6 hours after the learning, and the setup was identical to Group 1.1. The performance of the control group was plotted as the black line on the right panel. The movement errors of Group 3.2 and 3.3 were plotted in **(B)** and **(C)**, respectively. The setup of the decaying session for Group 3.2 was identical to Group 2.1, and the setup for group 3.3 was identical to that for Group 1.2.

Figure 6. Hand-paths from representative subjects observed on the first trials during the transfer session were compared between the experimental groups (color) and the control (black) in the left panels for 3.1, 3.2, and 3.3, respectively (**A-C**, left). Mean errors of the first

trial were compared (mean ± standard error) in the mid panels (**A-C**, middle), and the learning rates were plotted on the right (**A-C**, right). N.S. indicates not significant. *$p < 0.05$.

Figure 1

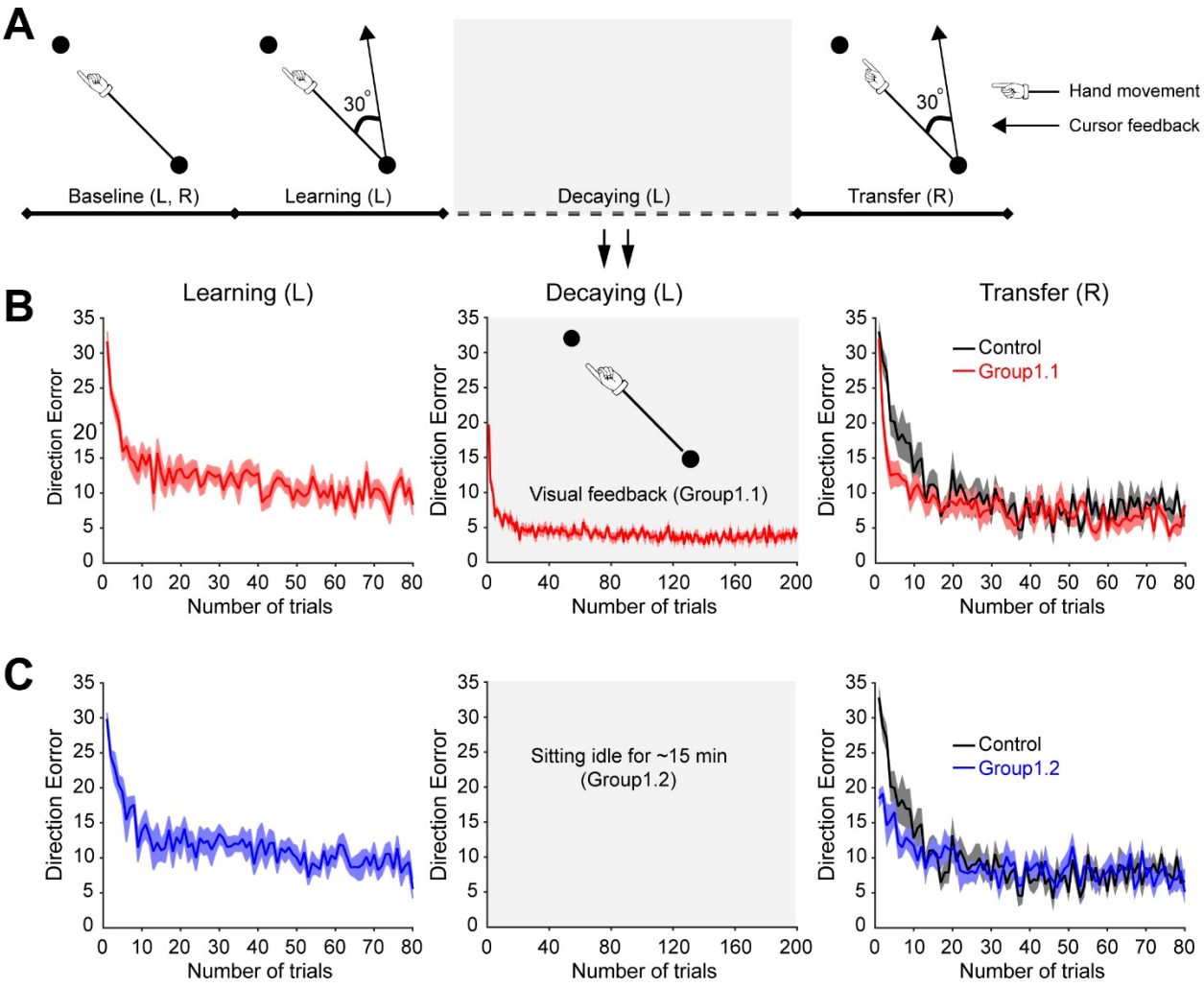

A
30°
30°
Hand movement
Cursor feedback
Baseline (L, R)
Learning (L)
Decaying (L)
Transfer (R)
B
Learning (L)
Decaying (L)
Transfer (R)
Direction Eorror
Number of trials
Visual feedback (Group1.1)
Control
Group1.1
C
Sitting idle for ~15 min
(Group1.2)
Control
Group1.2

Figure 2

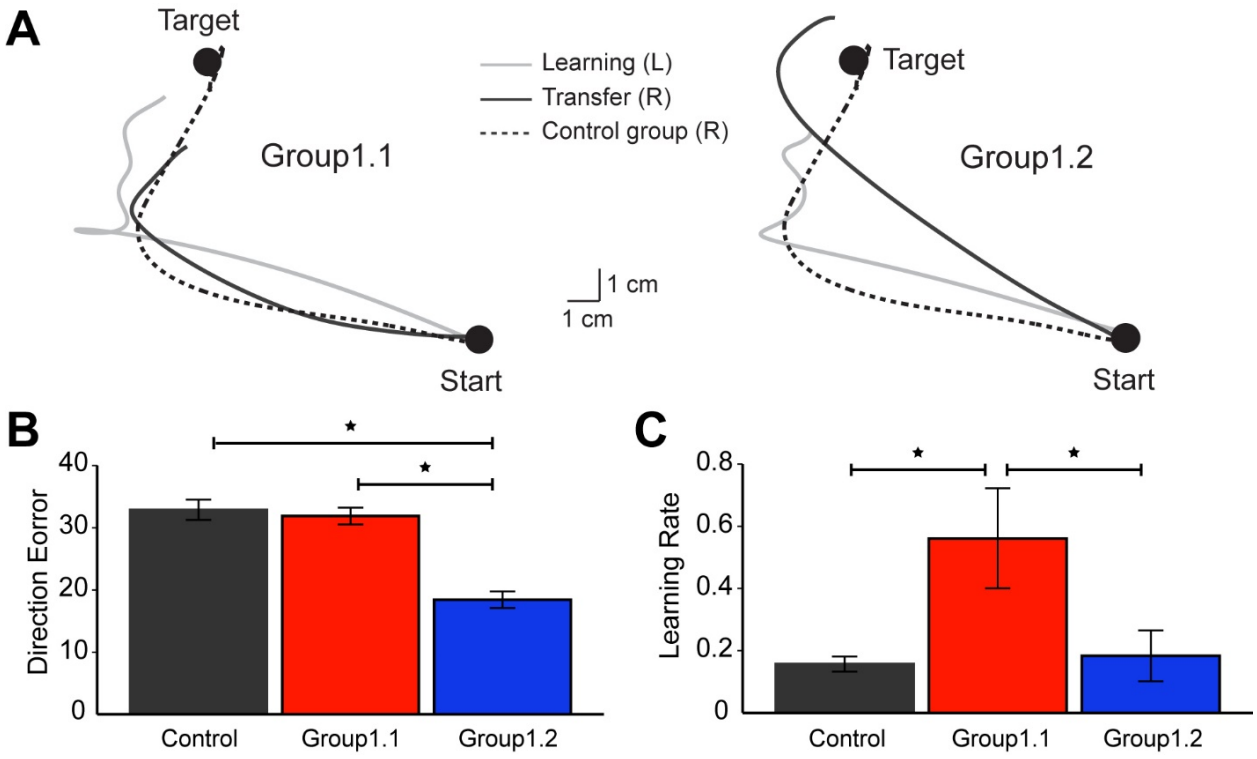

A
Target
Learning (L)
Transfer (R)
Control group (R)
Group1.1
1 cm
1 cm
Start
Target
Group1.2
Start
B
Direction Eorror
40
30
20
10
0
Control
Group1.1
Group1.2
C
Learning Rate
0.8
0.6
0.4
0.2
0
Control
Group1.1
Group1.2

Figure 3

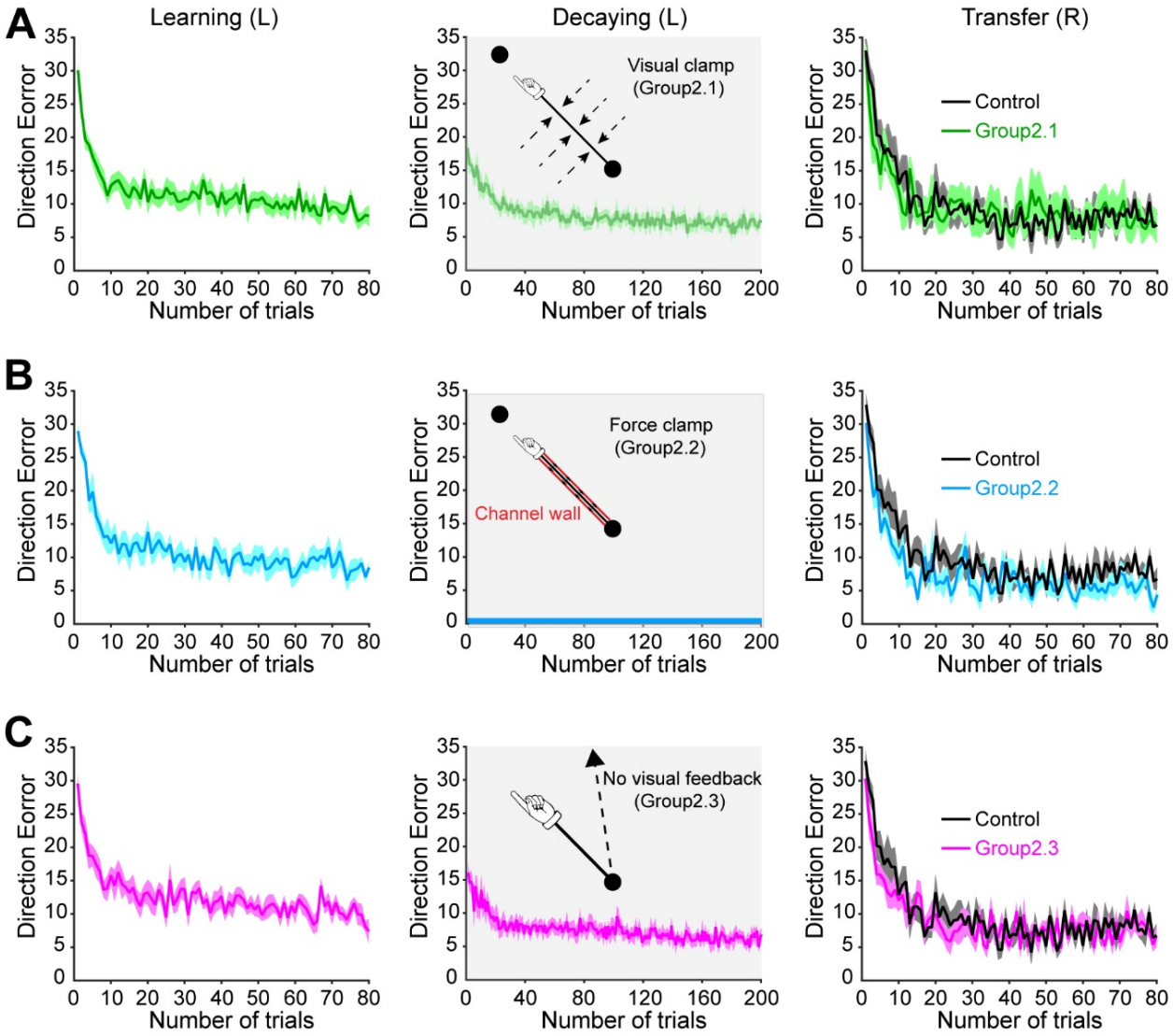

A
Learning (L)
Decaying (L)
Transfer (R)
Visual clamp
(Group2.1)
Control
Group2.1
B
Force clamp
(Group2.2)
Channel wall
Control
Group2.2
C
No visual feedback
(Group2.3)
Control
Group2.3
Direction Eorror
Number of trials

Figure 4

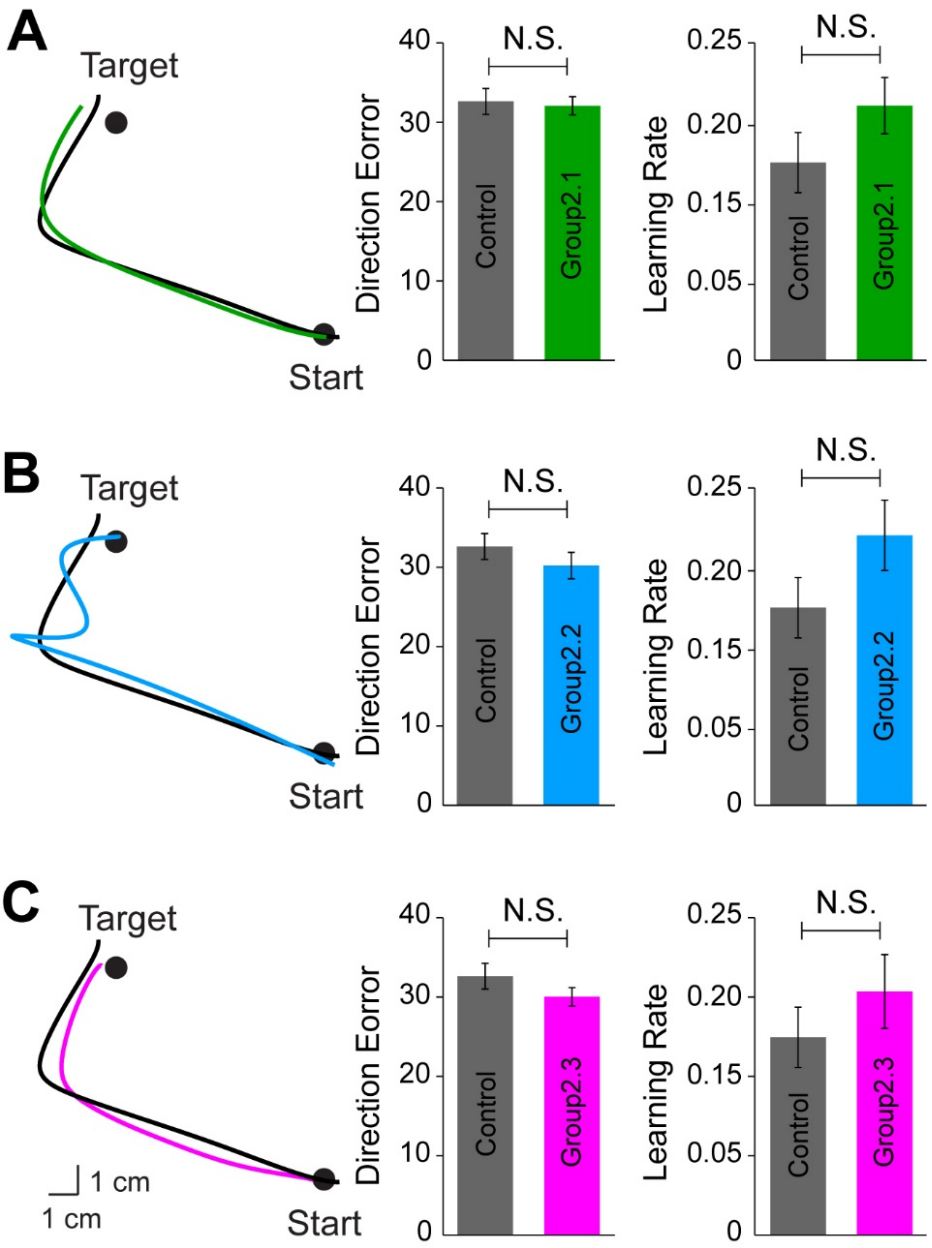

A
Target
Start
Direction Eorror
40
30
20
10
0
N.S.
Control
Group2.1
Learning Rate
0.25
0.20
0.15
0.05
0
N.S.
Control
Group2.1
B
Target
Start
Direction Eorror
40
30
20
10
0
N.S.
Control
Group2.2
Learning Rate
0.25
0.20
0.15
0.05
0
N.S.
Control
Group2.2
C
Target
1 cm
1 cm
Start
Direction Eorror
40
30
20
10
0
N.S.
Control
Group2.3
Learning Rate
0.25
0.20
0.15
0.05
0
N.S.
Control
Group2.3

Figure 5

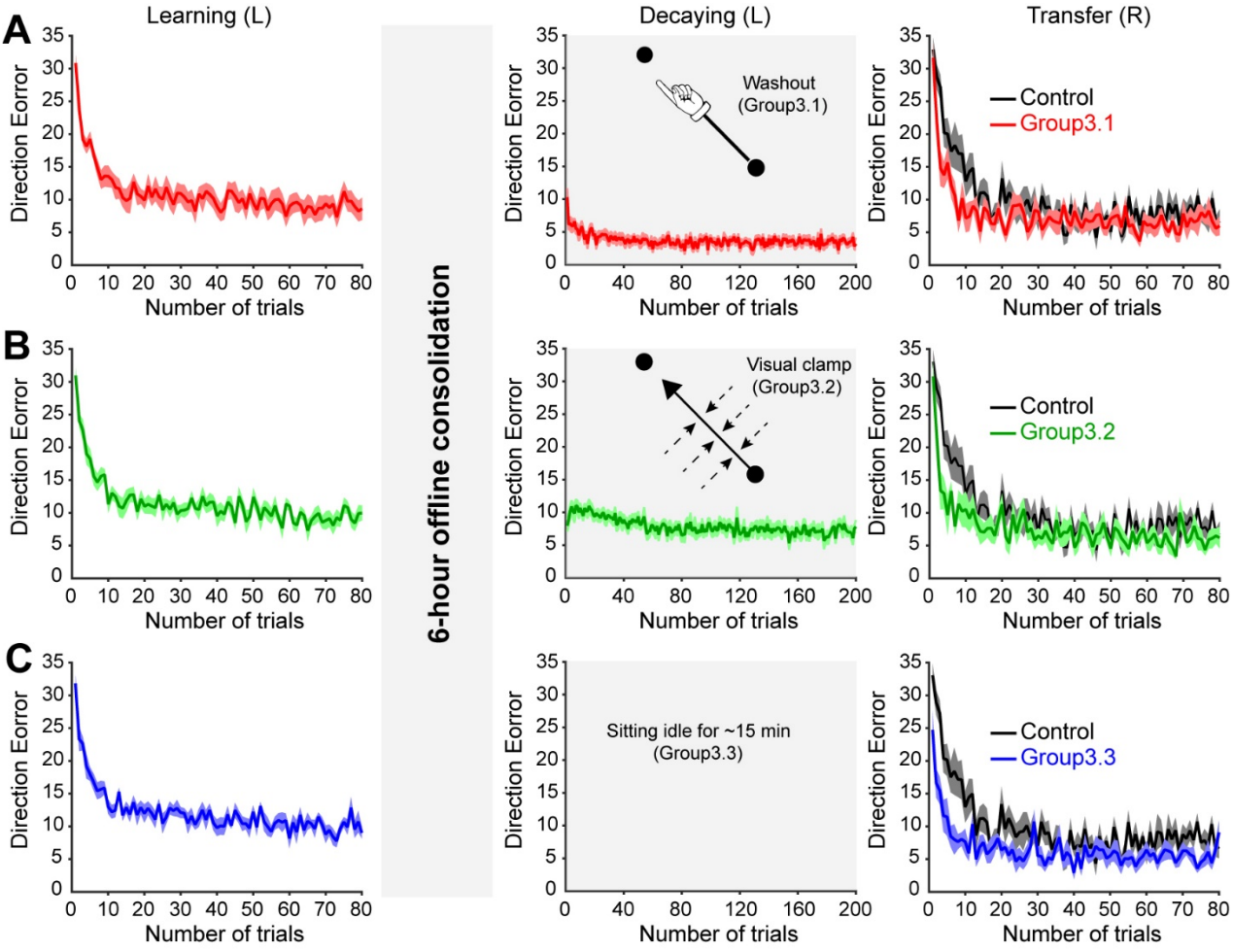
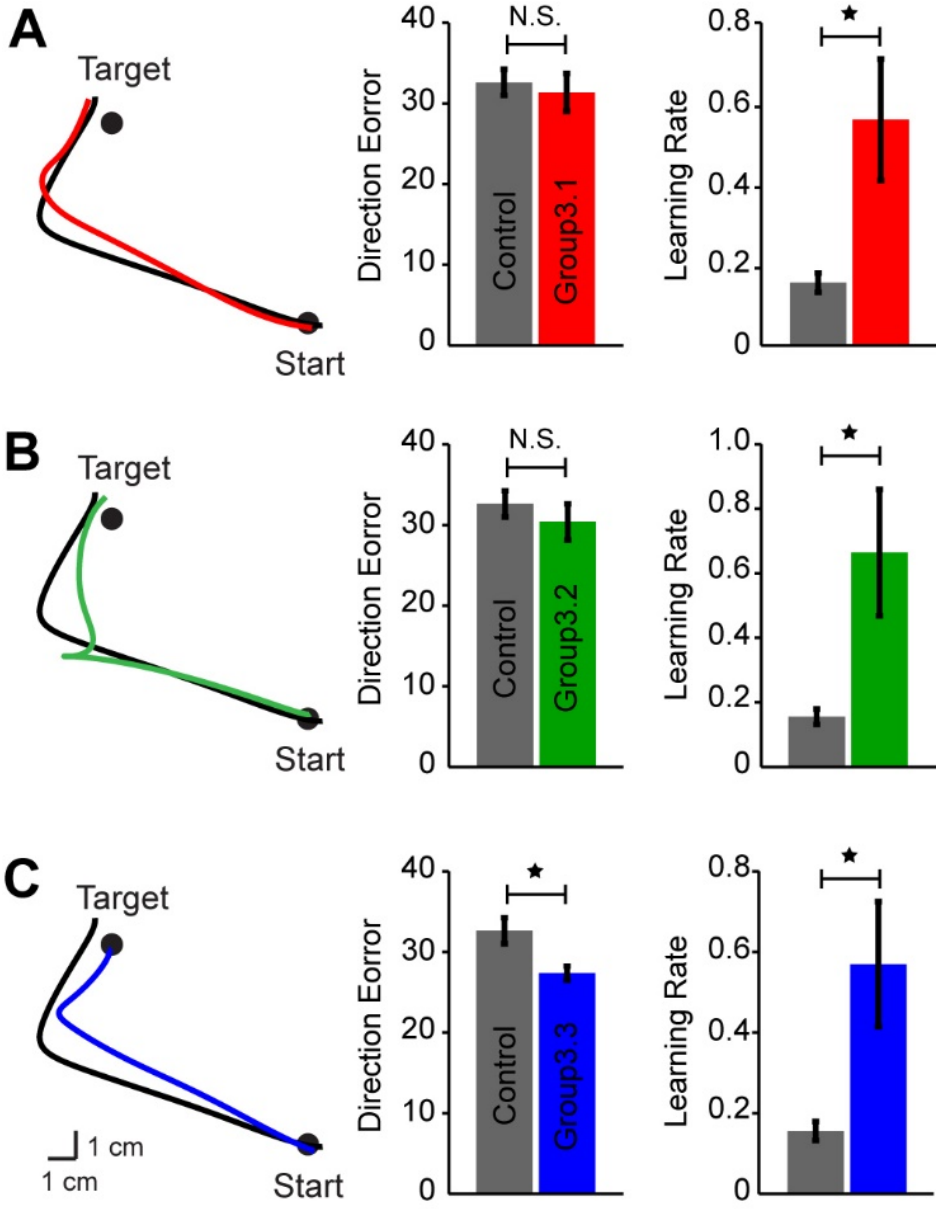

A
B
C
Learning (L)
Decaying (L)
Transfer (R)
Direction Eorror
Number of trials
6-hour offline consolidation
Washout
(Group3.1)
Visual clamp
(Group3.2)
Sitting idle for ~15 min
(Group3.3)
Control
Group3.1
Group3.2
Group3.3

Figure 6


A
Target
Start
Direction Eorror
40
30
20
10
0
N.S.
Control
Group3.1
Learning Rate
0.8
0.6
0.4
0.2
0
★
B
Target
Start
Direction Eorror
40
30
20
10
0
N.S.
Control
Group3.2
Learning Rate
1.0
0.8
0.6
0.4
0.2
0
★
C
Target
1 cm
1 cm
Start
Direction Eorror
40
30
20
10
0
★
Control
Group3.3
Learning Rate
0.8
0.6
0.4
0.2
0
★

Figures

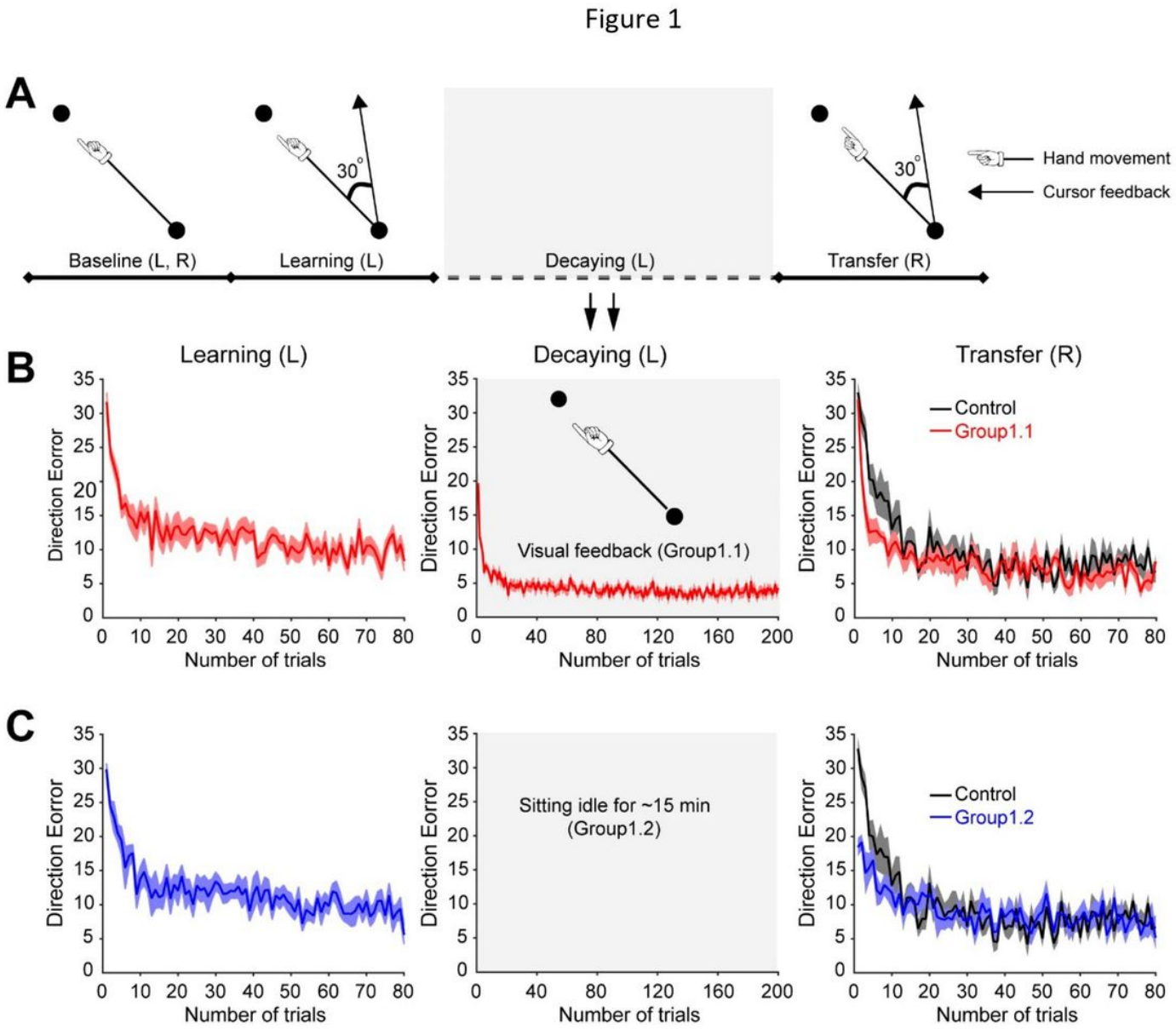


Figure 1

Protocols and the motor performance for Experiment 1. (A) The experimental protocol consisted of four sessions: baseline (veridical feedback), learning (30o CCW rotation), decaying, and transfer (30o CCW rotation with the opposite arm). The cursor feedback was CCW rotated by 30o from the hand-path in the learning and transfer sessions. (B) Mean time-course of the movement errors of the learning, decaying, and transfer sessions were plotted in red lines across trials for Group 1.1. Standard errors were represented as the shaded area plot. Veridical cursor feedback was provided during the decaying session as shown in the mid panel. The control group's right arm performance in the transfer session was plotted as black line in the right panel for comparison. (C) Mean time-course of the movement errors for Group

1.2 in blue lines. The subjects sit idle during the decaying session (mid panel). The control group's right arm performance was plotted in black in the right panel for comparison.

Figure 2

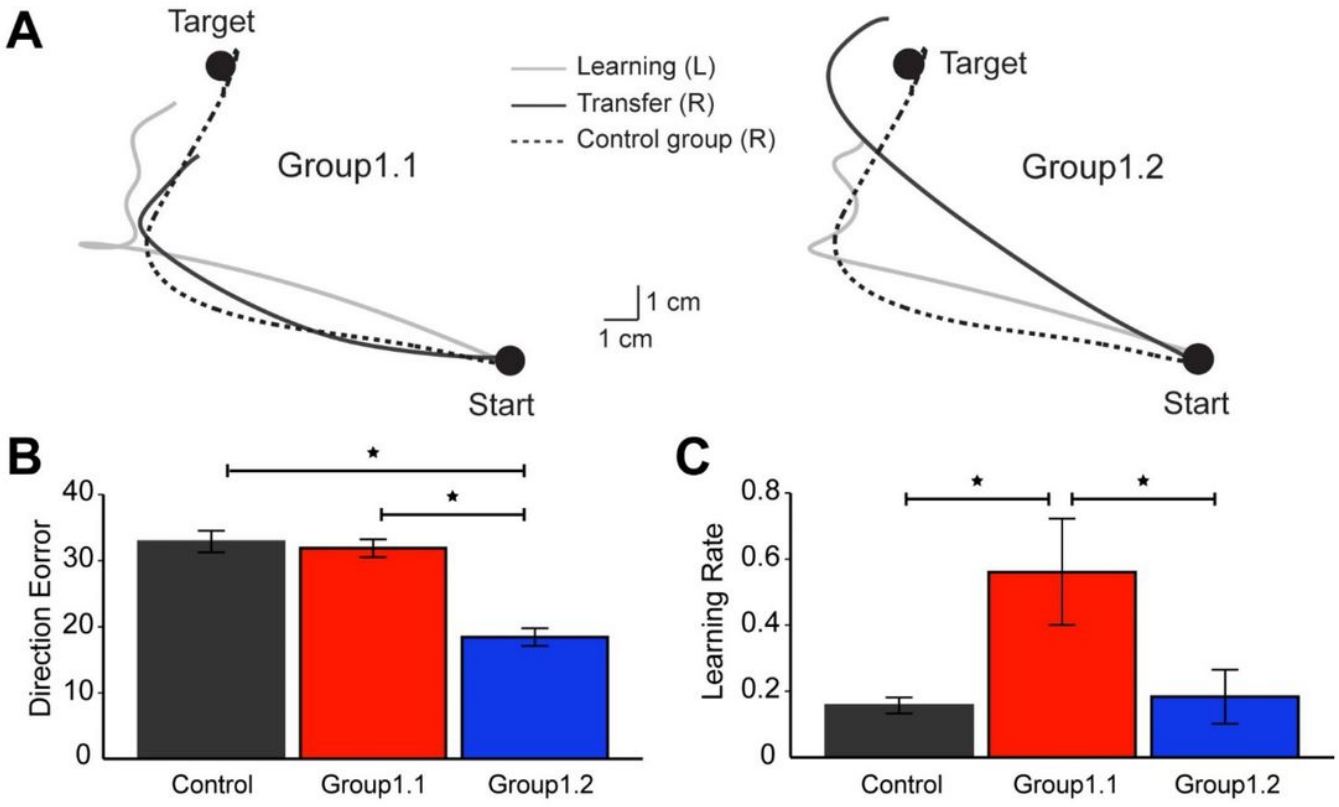


Figure 2

(A) Hand-paths from representative subjects observed on the first trials during the learning (gray) session and transfer (black) sessions for Group 1.1 (left) and 1.2 (right). The hand-path for the control group was plotted in dashed line. (B) Mean errors of the first trial in the transfer session for Group 1.1 (red), 1.2 (blue), and control (black) (mean ± standard error). (C) Comparison of learning rates in the transfer session for the control and Group 1.1 and 1.2. *$p < 0.05$.

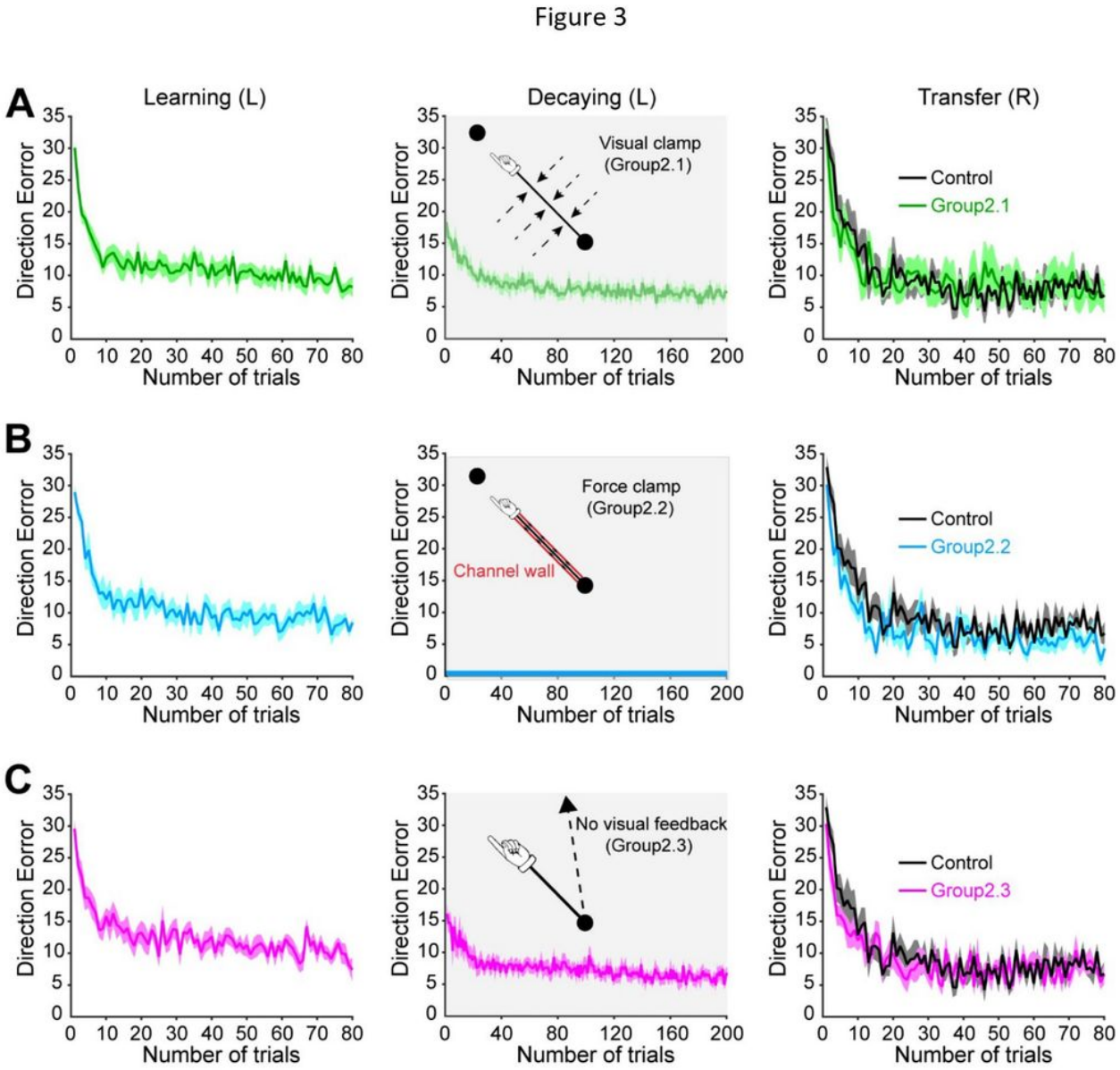


Figure 3

Performance for Experiment 2. (A) The movement errors of Group 2.1 in the learning, decaying, and transfer sessions were plotted in green lines and shaded areas (mean ± standard error). During the Decaying session, the cursor feedback was always on the straight line connecting the start and target circles. The black plot represented the control group's performance in the transfer session. The performance of Group 2.2 and 2.3 were depicted in (B) and (C), respectively. During the decaying session, a force channel restricted the hand-paths of Group 2.2 along the straight line connecting the start and target circles, so the hand-paths were always straight and accurate. No cursor feedback was provided for Group 2.3 during the decaying session, so the subjects reached towards the target based on their proprioception.

Figure 4

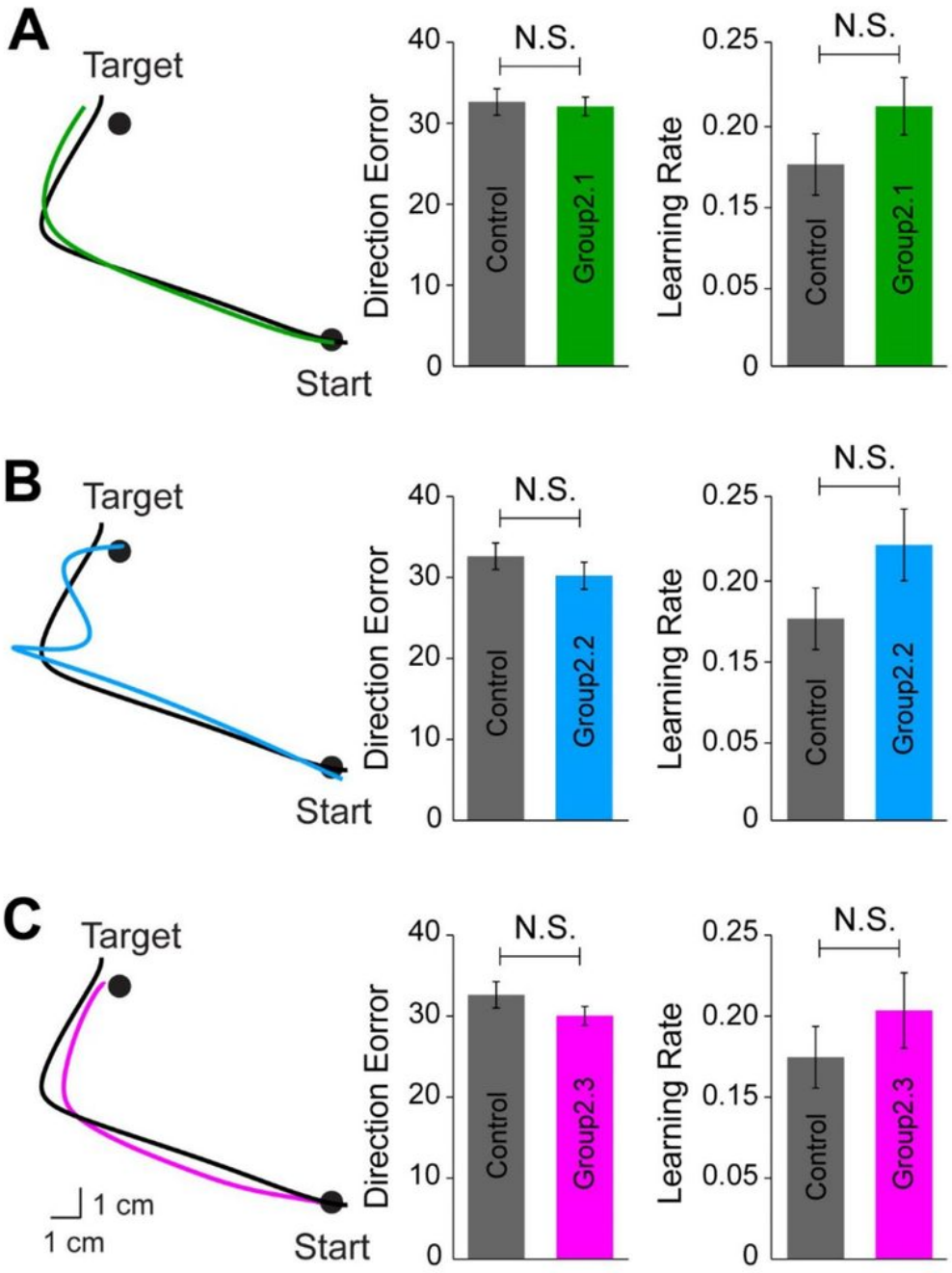


Figure 4

Hand-paths from representative subjects observed on the first trials during the transfer session were compared between the experimental groups (color) and the control (black) in the left panels for 2.1, 2.2, and 2.3, respectively (A-C, left). Mean errors of the first trial were plotted (mean ± standard error) in the mid panels (A-C, middle), and the learning rates were plotted on the right panels (A-C, right). N.S. indicates not significant ($p > 0.05$).

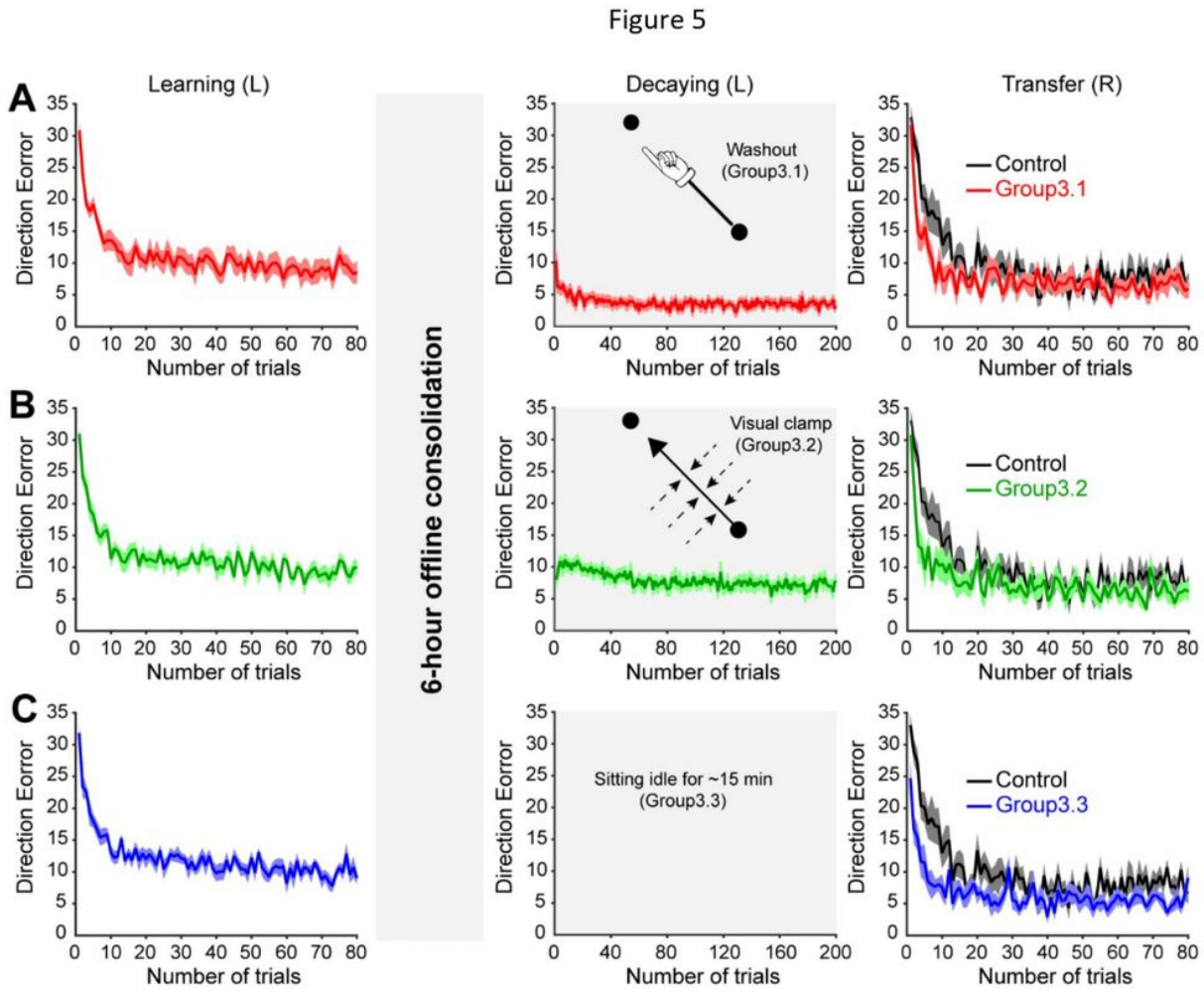


Figure 5

Performance of Experiment 3. (A) The movement errors of Group 3.1 in the learning, decaying, and transfer sessions were plotted in red lines and shaded areas (mean ± standard error). The decaying session was 6 hours after the learning, and the setup was identical to Group 1.1. The performance of the control group was plotted as the black line on the right panel. The movement errors of Group 3.2 and 3.3 were plotted in (B) and (C), respectively. The setup of the decaying session for Group 3.2 was identical to Group 2.1, and the setup for group 3.3 was identical to that for Group 1.2.

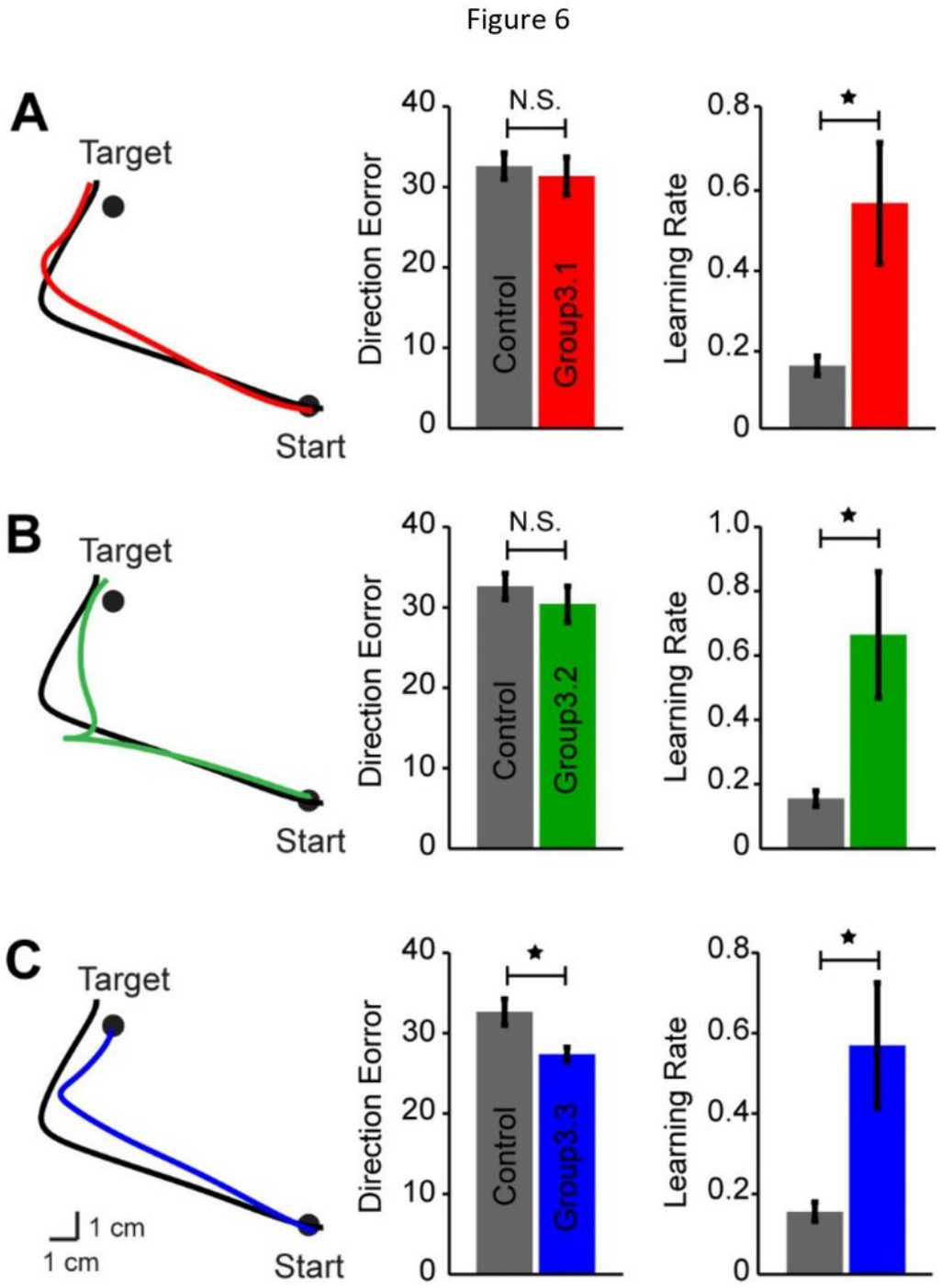


Figure 6

Hand-paths from representative subjects observed on the first trials during the transfer session were compared between the experimental groups (color) and the control (black) in the left panels for 3.1, 3.2, and 3.3, respectively (A-C, left). Mean errors of the first trial were compared (mean ± standard error) in the mid panels (A-C, middle), and the learning rates were plotted on the right (A-C, right). N.S. indicates not significant. *p < 0.05.