J Neurophysiol 123: 1180–1192, 2020.
First published February 26, 2020; doi:10.1152/jn.00524.2019.

RESEARCH ARTICLE | *Control of Movement*

Savings in sensorimotor adaptation without an explicit strategy

Cong Yin[4] **and Kunlin Wei**[1,2,3]
[1]*School of Psychological and Cognitive Sciences, Peking University, Beijing, China;* [2]*Beijing Key Laboratory of Behavior and Mental Health, Beijing, China;* [3]*Peking-Tsinghua Center for Life Sciences, Beijing, China; and* [4]*Capital University of Physical Education and Sports, Beijing, China*

Submitted 13 August 2019; accepted in final form 13 February 2020

Yin C, Wei K. Savings in sensorimotor adaptation without an explicit strategy. *J Neurophysiol* 123: 1180–1192, 2020. First published February 26, 2020; doi:10.1152/jn.00524.2019.—The hallmark of long-term retention of sensorimotor adaptation is a faster relearning when similar perturbations are encountered again. However, what processes underlie this saving effect is in debate. Though motor adaptation is traditionally viewed as a type of procedural learning, its savings has been recently shown to be solely based on a quick recall of explicit adaptation strategy. Here, we showed that adaptation to a novel error-invariant perturbation without an explicit strategy could enable subsequent savings. We further showed that adaptation to gradual perturbations could enable savings, which was supported by enhanced implicit learning. Our study provides supporting evidence that long-term retention of motor adaptation is possible without forming or recalling a cognitive strategy, and the interplay between implicit and explicit learning critically depends on the specifics of learning protocol and available sensory feedback.

NEW & NOTEWORTHY Savings in motor learning sometimes refers to faster learning when one encounters the same perturbation again. Previous studies assert that forming a cognitive strategy for countering perturbations is necessary for savings. We used novel experimental techniques to prevent the formation of a cognitive strategy during initial adaptation and found that savings still existed during relearning. Our findings suggest that savings in sensorimotor adaptation do not exclusively depend on forming and recalling an explicit strategy.

implicit learning; motor behavior; motor learning; savings; sensorimotor adaptation

INTRODUCTION

Sensorimotor adaptation occurs when the sensory consequence of motor action deviates from the expected consequence. Given that disturbances from the environment and from the body within are ubiquitous, sensorimotor adaptation serves as a fundamental learning mechanism for compensating the influences of these disturbances. Experimental studies typically apply visual or mechanical perturbations to human participants and investigate how people adjust their motor responses and recalibrate their sensory system to accommodate the effect of perturbations (Baddeley et al. 2003; Krakauer et al. 1999, 2000; Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994). Besides the immediate, and often transient, learning effect, adaptation also leads to long-lasting behavioral changes: people adapt faster when they encounter the same or similar perturbation a second time. This faster-relearning effect, which is termed savings (Ebbinghaus 1913), can be observed on the same day, overnight, or even after a year (Della-Maggiore and McIntosh 2005; Krakauer et al. 2005; Landi et al. 2011).

While savings is regarded as an indicator of long-term memory of motor adaptation, what is retained and retrieved during the readaptation is still in debate. One account proposed that memory of errors and its quick recognition during readaptation underlies the saving effect (Herzfeld et al. 2014), emphasizing enhanced sensitivity to (similar) errors during initial adaptation. This view is consistent with the traditional view that sensorimotor adaptation is an implicit, cerebellum-dependent, error-based learning process, which updates an internal forward model based on sensory prediction error (Izawa et al. 2012; Izawa and Shadmehr 2011; Mazzoni and Krakauer 2006; Miall and Wolpert 1996; Morton and Bastian 2006; Synofzik et al. 2008; Taylor et al. 2010; Tseng et al. 2007). The critical empirical support for this error-sensitivity account is that gradually induced perturbation, which effectively reduces the error available to the learner, would diminish savings (Herzfeld et al. 2014). A recent study further supports this account by showing that prior experience of errors, instead of the experience of the same action, is required to elicit savings (Leow et al. 2016).

Recent studies have found that multiple learning processes contribute to motor adaptation besides error-based learning (Huang et al. 2011). In particular, explicit cognitive strategies can account for a significant amount of learning, particularly during early adaptation and early readaptation (Mazzoni and Krakauer 2006; Taylor and Ivry 2011; Taylor et al. 2014). Accordingly, the second account of savings is that an explicit strategy is the main, if not the only, contributor to savings (Hadjiosif and Smith 2013; Huberdeau et al. 2019; Mazzoni and Krakauer 2006). For visuomotor rotation in reaching adaptation, people adapt to a novel visuomotor mapping, where the hand-controlled cursor moves with a rotated angle relative to the actual reaching direction. During adaptation, the explicit, cognitive strategy is to aim in the opposite direction of the rotation deliberately as opposed to aiming directly to the visual target. Thus, the explicit strategy can be operationally quantified as the verbally reported, rotated reaching direction before

Address for correspondence: K. Wei, School of Psychological and Cognitive Sciences, Peking Univ., No. 5 Yiheyuan Rd., Haidian District, Beijing, 100871, China (e-mail: wei.kunlin@pku.edu.cn).

each movement. Researchers have shown that faster readaptation in the visuomotor rotation is largely driven by a quick recall of this deliberate reaiming strategy (Haith et al. 2015; Morehead et al. 2015). During the initial adaptation, the reported aiming direction gradually deviates from the target direction, signifying the formation of explicit strategy. Consequently, savings observed during the readaptation is accompanied by a quick recall of the reaiming strategy. There is also other indirect evidence supporting the role of reaiming strategy in savings. For example, savings is absent when a reaiming strategy is not formed during initial adaptation due to overly small perturbation size (Morehead et al. 2015). People also have found that forcing participants to initiate movements rapidly could prevent the use of explicit strategy (Fernandez-Ruiz et al. 2011; Haith et al. 2015), consistent with the view that the reaiming strategy is associated with slow, deliberate cognitive processes. Furthermore, learning of an abrupt perturbation for just a couple of trials suffices to induce savings on the second day (Huberdeau et al. 2015); this fast learning is too short for implicit learning to take its full effect, which typically unfolds over tens of trials. Thus, this behavioral evidence leads to the theorization that savings in sensorimotor adaptation is mainly, if not solely, driven by forming and recall of an explicit strategy.

However, these two accounts, the error-sensitive account and the explicit strategy account, cannot be easily teased apart since most studies employed an abruptly introduced perturbation for the first and second learning epoch (Morehead et al. 2015). Thus, people simultaneously experience large and salient errors and form the explicit strategy, rendering dissociation of two competing accounts impossible. Here, by using a novel experimental technique that has been shown only to induce implicit learning, we show that savings is possible when no explicit strategy is developed during initial learning (*experiment 1*). Furthermore, though adaptation to gradually induced perturbations is regarded as implicit learning without savings (Herzfeld et al. 2014), our experiment, which requires participants to report their aiming directions, found robust savings after gradual adaptation (*experiment 2*). Some participants develop an explicit strategy during gradual adaptation, but other participants appear to adapt implicitly. Interestingly, their saving effect is supported by enhanced implicit learning during readaptation. Taken together, our study provides supporting evidence that forming or retrieving an explicit strategy is not a prerequisite for savings, and implicit learning and conceptual learning can enable long-term retention of motor adaptation.

MATERIALS AND METHODS

Participants. A total of 86 right-handed participants (41 males; average age = 22.47 ± 2.64 yr) were recruited for two separate experiments (n = 30, 56 for *experiments 1* and *2*, respectively). All participants were naïve to the purpose of the study, signed an institution-approved consent form, and were paid to participate. All experimental procedures were approved by the Institutional Review Board of Peking University.

Experimental setup. Each participant sat in a height-adjustable chair facing an LCD monitor, mounted vertically in front of them at eye level. The monitor had a 19-inch screen with a refreshing rate of 60 Hz. A digitizing tablet (Wacom Intuos 4) was placed on the horizontal desktop before the seated participant. A black paperboard placed horizontally underneath the monitor occluded vision of the hand. Each participant used the right hand to hold a digitizing pen whose position was measured in real time by the tablet with a resolution of 0.005 mm and a sampling frequency of 200 Hz. The data acquisition codes were written in MATLAB (MathWorks).

Basic movements. Participants were instructed to make rapid center-out shooting movements to eight radially arranged targets (white disks, 8 pixels in diameter) placed on a 5-cm-radius circle with an angular separation of 45°. The task required participants to use a hand-controlled cursor to slide through the target as accurately as possible. Their hand position was measured by the digitizing pen and presented as a cursor (a green disk, four pixels in diameter) when needed. At the beginning of each trial, a participant rested the digitizing pen on a 4-mm plastic disk glued onto the tablet. The disk was also used as an anchor to guide the participant to return the unseen finger to the starting position after each trial. A visual starting position, depicted as a yellow cross (4 pixels per line), was overlaid on the plastic disk. The hand cursor was only visible within 4 mm around the starting position. Once the finger stayed at the starting point for 100 ms, a target would appear, and a computer speaker sounded a beep to signal the participant to move. The feedback cursor was visible until the movement amplitude exceeded 5 cm. A beep sound was also played to signal the participant to bring the finger back to the starting position for the next trial once he/she stopped the movement. A low-pitched tone warned the participant when he/she reacted and moved too fast or too slow (reaction and movement time <200 ms or >800 ms). Before formal data collection, the participant practiced a few unperturbed trials to familiarize himself/herself with the required movement speed.

Experimental procedures. Both experiments employed the visuomotor rotation paradigm with similar procedures (Fig. 1*A*). We divided the experiment session into four consecutive phases: baseline, initial learning, washout, and relearning. In the baseline phase, participants received veridical cursor feedback for twenty 8-trial cycles, each cycle requiring the participant to move his finger to one of the eight targets once. The initial learning phase lasted for 40 cycles, with different types of learning, depending on the experimental condition. This phase was the critical phase for experimental manipulations. In the relearning phase, participants experienced an abrupt perturbation when the hand cursor was rotated 30° counter-clockwise (CCW) and remained rotated for 40 cycles. Between the initial learning phase and the relearning phase, we inserted the washout phase when participants moved without the cursor feedback for 10 cycles and then with veridical feedback for additional 20 cycles to wash out the apparent effect of initial learning (Galea et al. 2015).

Experiment 1 consisted of three groups whose initial learning involved different perturbations (Fig. 1*B*). The Control Group learned the same abrupt 30° CCW rotation as in the relearning phase. As shown by numerous previous studies (Krakauer et al. 1999, 2005; Zarahn et al. 2008). The Control Group should exhibit a saving effect, i.e., the relearning rate is larger than the initial learning rate, and this rate increase is largely driven by the formation of an explicit strategy (Haith et al. 2015). The second group, the Clamp Group, experienced different cursor feedback during initial learning: the hand cursor was never shown. Instead, a cursor moved synchronously with the hand but offset 30° CCW (Fig. 1*A*). The participants were fully informed that this cursor feedback would be invariant in direction, independent of their actual movement direction. They were also instructed to ignore the cursor feedback and move their hands directly toward the target. Nevertheless, people would involuntarily move their hands in the opposite direction of the clamped cursor, indicating a slow, implicit learning process (Morehead et al. 2017). Subsequently, we could examine whether pure implicit learning would lead to savings in the relearning phase. The third group, the Gradual Group, went through the same procedure as the Control Group, except for the initial learning phase: their 30° CCW rotation was gradually imposed with a rate of 0.0938° per trial. A previous study has shown that if the 30° perturbation is imposed gradually, people do not show savings when adapting to a subsequent abrupt 30° perturbation (Herzfeld et al.

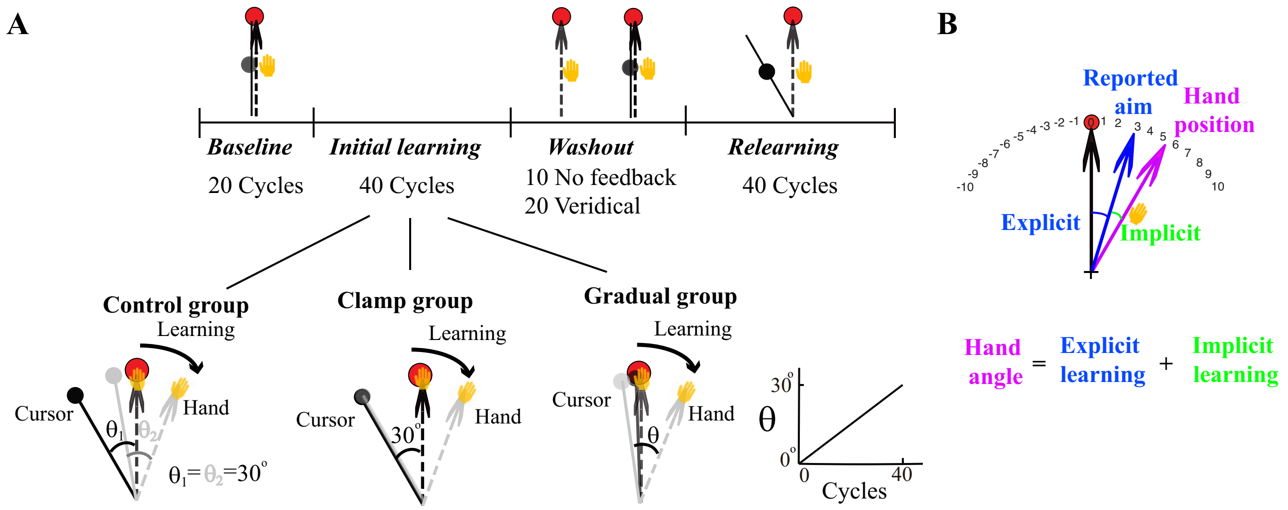

Fig. 1. Experimental design. *A*: four phases of trials for *experiments 1* and *2*, i.e., baseline, initial learning, washout, and relearning phases. Participants were randomly assigned to one of three groups for each experiment: Control Groups adapt to an abrupt 30° CCW visuomotor rotation during initial and relearning phases. As shown by schematic trajectories with two different shades of gray, the learning is indicated as the hand direction gradually rotates over trials to bring the cursor to land on the target. However, the angular perturbation (θ) remains 30° for Control Groups. The Clamp Groups move their unseen hands to the target while ignoring the time-locked, direction-invariant cursor feedback, which is 30° CCW to the target direction. As shown, their hands gradually rotates without their awareness while the cursor moves with a constant offset of 30° counterclockwise of the target. Gradual Groups adapt to visuomotor rotation, which gradually increases over trials. As shown, the angle θ between the hand and the cursor linearly increases over trial cycles, reaching 30° in the last, 40th cycle. *Experiment 2* but not *experiment 1* required the participants to report their aiming directions before each trial verbally. *B*: decomposition of explicit learning and implicit learning. On each trial in *experiment 2*, participants verbally reported the number corresponding to their aiming direction and then performed the movement. As shown, the numerated landmarks are displayed around the target. By assuming that the verbal report indicates explicit learning, the magnitude of implicit learning can be estimated by subtracting the aiming angle from the actual hand angle (Taylor et al. 2014).

2014). However, the two major accounts of savings appear to be capable of explaining this absence of savings: the error-sensitivity account could argue that gradual perturbations do not give participants enough exposure of salient errors; the explicit strategy account could argue that people could not develop reaiming strategy with small errors, though this explanation has not been tested. *Experiment 1* included the Gradual Group to check whether we could replicate previous findings: if savings were absent, we would go a step further to examine whether a failure of forming or recalling an explicit strategy underlies the absence of savings in *experiment 2*.

Experiment 2 used a similar protocol to *experiment 1* with three newly recruited groups of participants. The critical difference was that all participants would need to verbally report their aiming direction before each shooting movement (Fig. 1*B*). As the aiming report is typically associated with increased variance in reaching directions, we increased the number of participants per group from 10 to 14 for both $\text{Control}_{\text{report}}$ and $\text{Clamp}_{\text{report}}$ Groups. For the $\text{Gradual}_{\text{report}}$ Group, we found that about half of the participants did not form any reaiming strategy throughout the initial learning phase when the visuomotor rotation gradually ramped to 30°. We doubled the number of participants for this group to 28 to have enough samples for both subgroups, whose explicit learning was either present or absent during initial learning. Note, the assignment of these two subgroups ($\text{Gradual}_{\text{strategy}}$ and $\text{Gradual}_{\text{implicit}}$) were not experimentally controlled but borne out of participants' actual performance.

The three groups differed slightly in the requested verbal reports of aiming directions. $\text{Control}_{\text{report}}$ Group and $\text{Gradual}_{\text{report}}$ Group were required to report their aiming direction for every trial except the first 10 baseline cycles and the first 10 washout cycles (without veridical feedback). The first 10 baseline cycles allowed the participants to familiarize themselves with the reaching movement, and the last 10 baseline cycles allowed them to familiarize themselves with the aiming report. Different from these two groups, the $\text{Clamp}_{\text{report}}$ Group skipped the verbal report for the initial learning since they were instructed to go straight to the visual target. Using the aiming report, we can quantify explicit learning and then estimate implicit learning, which is defined as the difference between the actual movement direction and the aiming direction (Taylor et al. 2014). Importantly, we can also probe what underlies savings during initial learning and relearning.

To facilitate the report of aiming, each target was surrounded by a ring of 21 numbered visual landmarks spaced 5.625° apart (labeled from −10 to 10). The numbers were increasingly negative and increasingly positive from the target in the counterclockwise and clockwise directions, respectively (Fig. 1*B*). Before each movement, the participants were instructed to report the landmark number they planned to move to verbally. The reported aiming direction was recorded by an experimenter. The eight targets were laid on an 8-cm-radius circle instead of 5 cm in *experiment 1* to display discernible landmarks. If the participant reported their aiming direction too slow (>1,000 ms), a beep sound was played to remind them.

Data analysis. The direction of the shooting movement indicated the participants' adaptive response to the visuomotor rotation, which was determined by computing the direction of the vector spanning from the starting position to the position of the hand at the peak outward velocity. We computed the relative angle (abbrev. angle) between the movement direction and the target direction. A positive angle indicates a clockwise rotation that compensates the CCW rotation perturbation. We also computed each participant's direction biases associated with moving to different targets based on the last 10 baseline cycles. These direction-specific baseline biases were subtracted from the movement directions obtained in later learning phases.

In *experiment 1*, the Control Group reduced their directional errors most rapidly within the first eight cycles. We compared their performance between the initial learning phase and the relearning phase cycle by cycle using paired *t* tests. After the 8th cycle, their performance reached a plateau without a significant difference between these two phases. Thus, we used the window from *cycle 2* to *cycle 8* to compute the learning rate and relearning rate for all of the groups in *experiment 1*. The learning rate was operationally defined as the average angle within the window. Thus, the larger the angle, the faster people adapted to the perturbation initially. The difference in the learning rate between the initial learning phase and the relearning phase served as a measure of savings (for similar treatments, see Huberdeau et al. 2015; Krakauer et al. 2005; Yin et al. 2016). We also verified that our results were not sensitive to the choice of window size, as all our major findings did not change if we increased the window size, e.g., to *cycle 12*. For *experiment 2*, we used the reported aiming direction as a proxy of explicit learning and decomposed the savings into explicit and implicit components. Subsequently, the amount of implicit learning was estimated as the difference between the actual angle and the reported aiming angles (Taylor et al. 2014). The window for savings spanned from the 2nd cycle to the 16th cycle, since the $\text{Control}_{\text{report}}$ Group showed different performance between the initial learning and relearning phase until the 16th cycle. We calculated the explicit and implicit learning components within the window for savings. As *experiments 1* and *2* used a different window size for savings, we also examined whether our results would be sensitive to the choice of window size. We used a single window size for all the group comparisons and varied the size from 2–8 to 2–20 cycles. We confirmed that the change of window size would not change the outcomes of inferential statistics, with only one exception: when compared with the $\text{Control}_{\text{report}}$ Group, the $\text{Clamp}_{\text{report}}$ Group showed significant larger explicit learning using the 2–16-cycle window, but this difference became marginally significant ($P = 0.07$) when using the 2–8-cycle window. Besides learning rate and savings, for learning with clamped feedback and abrupt perturbations, we also quantified the learning extent by computing the average angle over its last five cycles. As the washout period was relatively short, participants showed residual adaptation before the relearning phase. We analyzed the relearning performance by subtracting the residual adaptation (the average angle over the last five cycles during washout) and confirmed that all major findings still hold.

We were interested in whether the learning rate could be enhanced after participants were exposed to different types of initial learning. Thus, the relearning rates of the groups who experienced either error-clamp learning or gradual learning were compared with the Control Groups. For *experiments 1* and *2*, we compared the relearning phase of these test groups with the initial learning phase of the Control Group to examine possible saving effect when all these groups encountered an abrupt 30° rotation for the first time. These tests were performed with one-way ANOVA with independent samples. Note, the same group comparison was also performed between the relearning phase of the test groups and the relearning phase of the Control Group to examine whether their learning rates increased to a similar level. Planned contrasts were conducted to specifically compare each test group's performance with that of the Control Group. Furthermore, the saving effect within a Control Group was examined by paired *t* tests (two-tailed), in which their initial learning and relearning was compared. Independent *t*-tests were used when directly comparing two samples when applicable. We also reported the Bayes factor (B) when a *t*-test failed to detect a significant difference (Morey and Wagenmakers 2014). The normality assumption was examined before *t*-tests and ANOVA. All dependent variables satisfied the assumption. Before the statistical analyses, we excluded trials in which the movement direction was more than three standard deviations from the mean for that cycle. This resulted in an average removal of less than 0.5% of the trials per participant. The significance level was set at $\alpha = 0.05$.

RESULTS

In *experiment 1*, we first established that participants showed a substantial saving effect after participants only implicitly adapted to error-clamped feedback. This suggests that savings can be elicited without showing any strategic learning during initial learning. In *experiment 2*, participants showed savings after gradual learning only when they were additionally required to report their aiming directions before each trial. Decomposing the total learning into explicit and implicit components, we found that this faster readaptation was mainly caused by expedited implicit learning, independent of whether participants formed an explicit strategy during initial learning.

Experiment 1: adaptation without aiming reports. As expected, the Control Group showed significant savings when participants learned the abrupt 30° perturbation for a second time. After the baseline phase, participants gradually learned the perturbation by increasing their movement angle to 30°, which was the size of the visuomotor rotation (Fig. 2*A*). The learning rate, defined as the average angle over the 2nd–8th learning cycles, was 14.53 ± 1.99° (average ± SE, same below). During the washout phase, the angle gradually decreased toward a baseline of 0°, indicating that their adaptation diminished with time and veridical cursor feedback. During the relearning phase, the learning rate increased to 23.85 ± 1.29°, which was significantly faster than the initial learning rate [paired *t* test, $t_{(9)} = 6.53$, $P < 0.001$] and demonstrating a classical saving effect.

Compared with the Control Group, the Clamp Group experienced an initial learning phase with error-clamped feedback rather than with an abrupt 30° visuomotor rotation. During error-clamp learning, they showed a gradual shift of movement

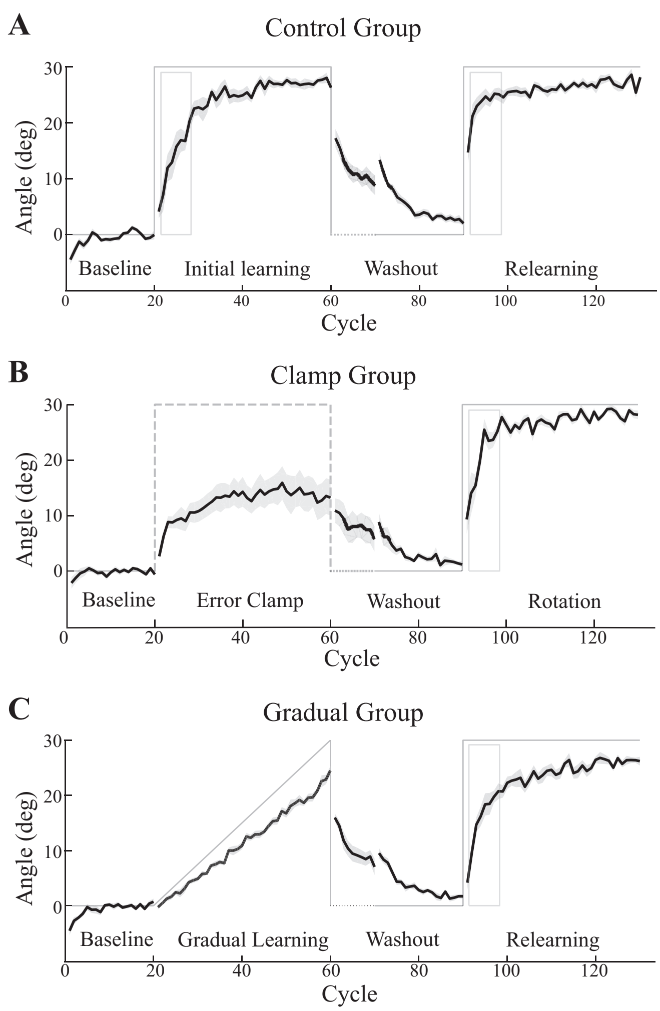

Fig. 2. Learning data of the Control Group (*A*), Clamp Group (*B*) and Gradual Group (*C*) in *experiment 1*. The gray lines denote perturbation. The gray boxes indicate the windows for calculating the learning rate and relearning rate. The shaded areas denote means ± SE.

direction in the opposite direction of the rotated, clamped cursor (Fig. 2*B*). Note this learning-related change was not voluntarily controlled, as participants intended to move their unseen hand straight to the visual target, but their hand involuntarily deviated from their intended movement direction, which is regarded as one type of implicit learning (Morehead et al. 2017). It led to a hand deviation of 13.18 ± 2.98° during the last five cycles, similar to what has been previously reported (Morehead et al. 2017). Our Gradual Group adapted to gradual perturbations during their initial learning, with an average angle of 24.50 ± 0.78° over the last cycle in this phase (Fig. 2*C*). Thus, the Gradual Group experienced the largest visual target error of 5.50 ± 0.78°, which was far smaller than the size of the rotation that would be imposed during the relearning phase.

After the washout phase, the Clamp Group, but not the Gradual Group, showed significant savings during the relearning phase when they encountered an abrupt 30° rotation (Fig. 3).

The relearning rate was 20.98 ± 1.30° and 16.84 ± 1.32° for the Clamp Group and the Gradual Group, respectively. When comparing to the initial learning rate of the Control Group, one-way ANOVA revealed a significant group difference ($F_{2,\,27}$ = 4.35, P = 0.02). Planned contrasts indicated that only the Clamp Group learned significantly faster than the Control Group [$t_{(27)}$ = 2.91, P = 0.01]. When comparing to the relearning rate of the Control Group, one-way ANOVA also showed a significant group difference ($F_{2,\,27}$ = 7.32, P = 0.003). Planned contrasts indicated that the Gradual Group learned significantly slower than the Control Group [$t_{(27)}$ = 3.81, P = 0.001]. Thus, when compared with the performance of the Control Group, initial learning with the clamped feedback, but not with gradual perturbations, led to savings. Notably, participants did not adapt with explicit strategy during clamp learning.

Experiment 2: adaptation with aiming reports. With the aiming report, the Control$_{report}$ Group in *experiment 2* showed a similar saving effect as the Control Group in *experiment 1* (Fig. 4*A*). Participants adapted significantly faster during relearning with an initial learning rate of 17.21 ± 1.50° and a relearning rate of 25.94 ± 1.06° (paired *t*-test, $t_{(13)}$ = 5.31, P < 0.001). We also quantified the relative contribution of the explicit and implicit learning to the adaptation performance. Similar to previous research (Bond and Taylor 2015; Morehead et al. 2015; Taylor et al. 2014), the initial learning phase was characterized by a rapid increase of explicit learning and a gradual increase of implicit learning (Fig. 4*A*). In contrast, the relearning phase was characterized by a more rapid increase of explicit learning and a relatively slow implicit learning. Thus, the faster relearning rate is predominantly caused by faster explicit learning: the explicit learning was significantly larger in the relearning phase than in the initial learning phase [20.72 ± 2.43° and 9.42 ± 1.96°, $t_{(13)}$ = 4.59, P < 0.001], while no difference was found for the implicit learning [5.22 ± 2.96° and 7.79 ± 1.67°, $t_{(13)}$ = −0.91, P = 0.38, B = 0.39]. Overall, these results replicated the previous finding that when experiencing an abrupt perturbation twice, the saving effect is largely caused by the recall of the acquired aiming strategy (Morehead et al. 2015).

As in *experiment 1*, the Clamp$_{report}$ Group exhibited implicit learning with the clamped feedback, with an average angle of 10.02 ± 1.23° over the last five cycles (Fig. 4*B*). This learning did not differ from that in *experiment 1* [$t_{(22)}$ = 1.09, P = 0.29, B = 0.58].

Aiming reports indicated that different participants in the Gradual$_{report}$ Group behaved differently when adapting to gradual perturbations. We found that 16 out of the 28 participants generated an aiming strategy during the gradual learning phase, as their reported aiming direction differed from the actual target direction (Fig. 4*C*). In contrast, the remaining 12 participants always reported moving straight to the target, suggesting a lack of strategy use (Fig. 4*D*). Thus, we separately analyzed these two subgroups of participants (Gradual$_{strategy}$ and Gradual$_{implicit}$ Groups). The 16 participants in the Gradual$_{strategy}$ Group started to develop an aiming strategy at varying times during initial learning, ranging from the 1st to the 29th cycle, with a median value of 18.5. The average performance error (the angular deviation from the target) they saw when they started to reaim their reach was 2.82 ± 0.58°. The maximum reaiming angle ranged from 0.7° to 16.88°, with a median of 5.27°. Thus, these participants showed a large variance of their reaiming behavior in both timing and magni-

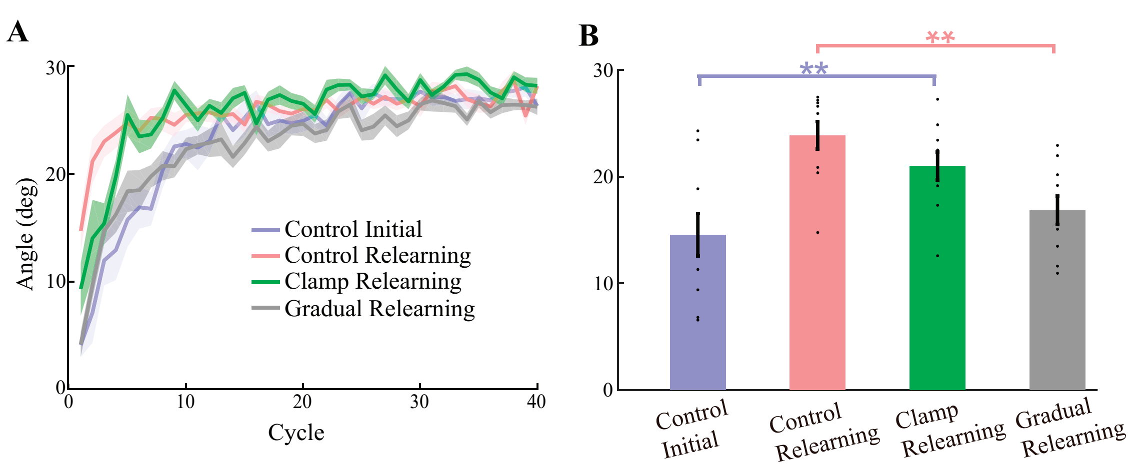

Fig. 3. Comparison of the learning rates from different groups in *experiment 1*. *A*: learning curves in the relearning phase of the Clamp Group and the Gradual Group plotted along with the two learning curves from the Control Group. The shaded areas denote means ± SE *B*: average learning rate (error bars denote means ± SE) in each group. Each dot represents a participant. ***P* < 0.01.

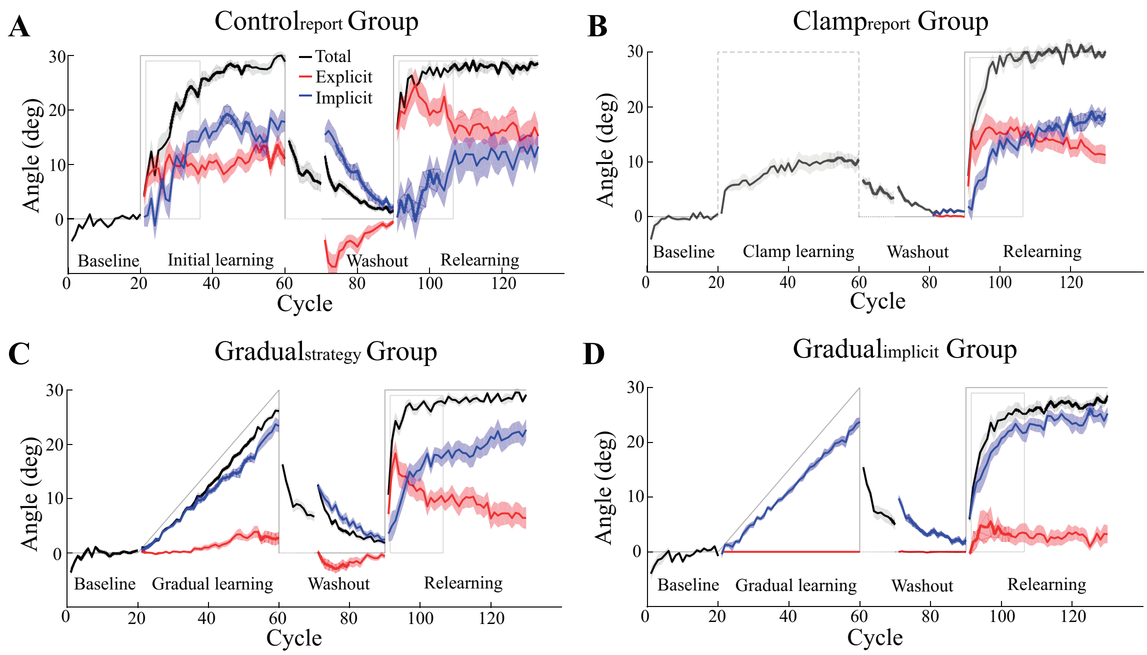

Fig. 4. Learning data of the $\text{Control}_{\text{report}}$ Group (*A*), $\text{Clamp}_{\text{report}}$ Group (*B*), $\text{Gradual}_{\text{strategy}}$ Group (*C*), and $\text{Gradual}_{\text{implicit}}$ Group (*D*) in *experiment 2*. Total learning, implicit learning, and explicit learning are plotted as a function of trial cycles. The gray lines denote perturbation. The gray boxes indicate the windows for calculating the learning rate and relearning rate. The shaded areas denote means ± SE.

tude. Nevertheless, their explicit learning was merely 2.99 ± 0.86° for the last 10 cycles during the initial learning phase.

After washout, all three test groups, including the $\text{Clamp}_{\text{report}}$ Group, the $\text{Gradual}_{\text{strategy}}$ Group, and the $\text{Gradual}_{\text{implicit}}$ Group, exhibited savings when compared with the performance of the $\text{Control}_{\text{report}}$ Group (Fig. 5*A*). Their relearning rate was 25.39 ± 1.22°, 26.05 ± 0.80°, and 22.02 ± 1.01°, respectively (Fig. 5*D*). When comparing to the initial learning rate of the $\text{Control}_{\text{report}}$ Group, one-way ANOVA found a significant group difference ($F_{3,\ 52} = 12.62$, $P < 0.001$). Planned contrasts indicated that the $\text{Clamp}_{\text{report}}$ Group [$t_{(52)} = 5.01$, $P < 0.001$], the $\text{Gradual}_{\text{strategy}}$ Group [$t_{(52)} = 5.59$, $P < 0.001$], the $\text{Gradual}_{\text{implicit}}$ Group [$t_{(52)} = 2.83$, $P = 0.01$] learned significantly faster than the $\text{Control}_{\text{report}}$ Group. When comparing to the relearning rate of the $\text{Control}_{\text{report}}$ Group, one-way ANOVA also found a significant difference between groups ($F_{3,\ 52} = 3.14$, $P = 0.03$). Planned contrasts indicated that all test groups did not differ, except that the $\text{Gradual}_{\text{implicit}}$ Group learned slower than the $\text{Control}_{\text{report}}$ Group [$t_{(52)} = -2.60$, $P = 0.01$]. These results indicated that all the test groups improved their learning rate during the relearning phase, although the effect of the $\text{Gradual}_{\text{implicit}}$ Group was not as pronounced as other groups.

We then compared the explicit component between the test groups and the control group (Fig. 5*B*). Their explicit learning rate within the saving window was 15.09 ± 1.89°, 12.31 ± 1.81°, and 3.56 ± 1.56° for the $\text{Clamp}_{\text{report}}$ Group, the $\text{Gradual}_{\text{strategy}}$ Group, and $\text{Gradual}_{\text{implicit}}$ Group, respectively (Fig. 5*D*). When comparing to the initial learning rate of the $\text{Control}_{\text{report}}$ Group, one-way ANOVA showed a significant group difference ($F_{3,\ 52} = 6.64$, $P = 0.001$). Planned contrasts revealed that the $\text{Clamp}_{\text{report}}$ Group had significantly more explicit learning [$t_{(52)} = 2.18$, $P = 0.03$] but the $\text{Gradual}_{\text{implicit}}$ Group had significantly less explicit learning than the $\text{Control}_{\text{report}}$ Group [$t_{(52)} = -2.17$, $P = 0.04$]. When comparing to the relearning rate of the $\text{Control}_{\text{report}}$ Group, one-way ANOVA showed a significant group difference again ($F_{3,\ 52} = 12.07$, $P < 0.001$). Planned contrast revealed that the $\text{Clamp}_{\text{report}}$ Group [$t_{(52)} = -2.02$, $P = 0.049$], the $\text{Gradual}_{\text{strategy}}$ Group [$t_{(52)} = -3.12$, $P = 0.003$], and the $\text{Gradual}_{\text{implicit}}$ Group ($t_{(52)} = -5.92$, $P < 0.001$) had significantly less explicit learning when compared with the $\text{Control}_{\text{report}}$ Group. Taken together, the $\text{Clamp}_{\text{report}}$ Group, but not the two gradual learning groups, relied on explicit learning when they showed their savings during relearning. In fact, the explicit learning in the $\text{Gradual}_{\text{implicit}}$ Group was significantly reduced.

We also compared the contribution of implicit component among all test groups and the $\text{Control}_{\text{report}}$ Group (Fig. 5*C*). Their implicit learning rate within the saving window was 10.30 ± 1.17°, 13.74 ± 1.53°, and 18.46 ± 1.25° for the $\text{Clamp}_{\text{report}}$ Group, the $\text{Gradual}_{\text{strategy}}$ Group, and the $\text{Gradual}_{\text{implicit}}$ Group, respectively (Fig. 5*D*). When compared with the initial learning rate of the $\text{Control}_{\text{report}}$ Group, one-way ANOVA found a significant group difference ($F_{3,\ 52} = 9.41$, $P < 0.001$). Planned contrasts revealed that the $\text{Gradual}_{\text{strategy}}$ Group [$t_{(52)} = 3.00$, $P = 0.004$] and the $\text{Gradual}_{\text{implicit}}$ Group [$t_{(52)} = 5.01$, $P < 0.001$] had significantly larger implicit learning than the $\text{Control}_{\text{report}}$ Group. When compared with the relearning rate of the $\text{Control}_{\text{report}}$ Group, one-way ANOVA also found a significant group difference ($F_{3,\ 52} = 8.17$, $P < 0.001$). Planned contrasts revealed that, again, the $\text{Gradual}_{\text{strategy}}$ Group [$t_{(52)} = 3.29$, $P = 0.002$] and the $\text{Gradual}_{\text{implicit}}$ Group [$t_{(52)} = 4.75$, $P < 0.001$] had significantly larger implicit learning than the $\text{Control}_{\text{report}}$ Group. Together, these results indicated that implicit learning was enhanced for the two gradual learning groups, while explicit learning was enhanced for the $\text{Clamp}_{\text{report}}$ Group.

The $\text{Gradual}_{\text{strategy}}$ Group did not show an enhanced explicit learning rate within the window of savings, but we observed a sign of possible recall of explicit strategy (Fig. 5*B*, indicated by

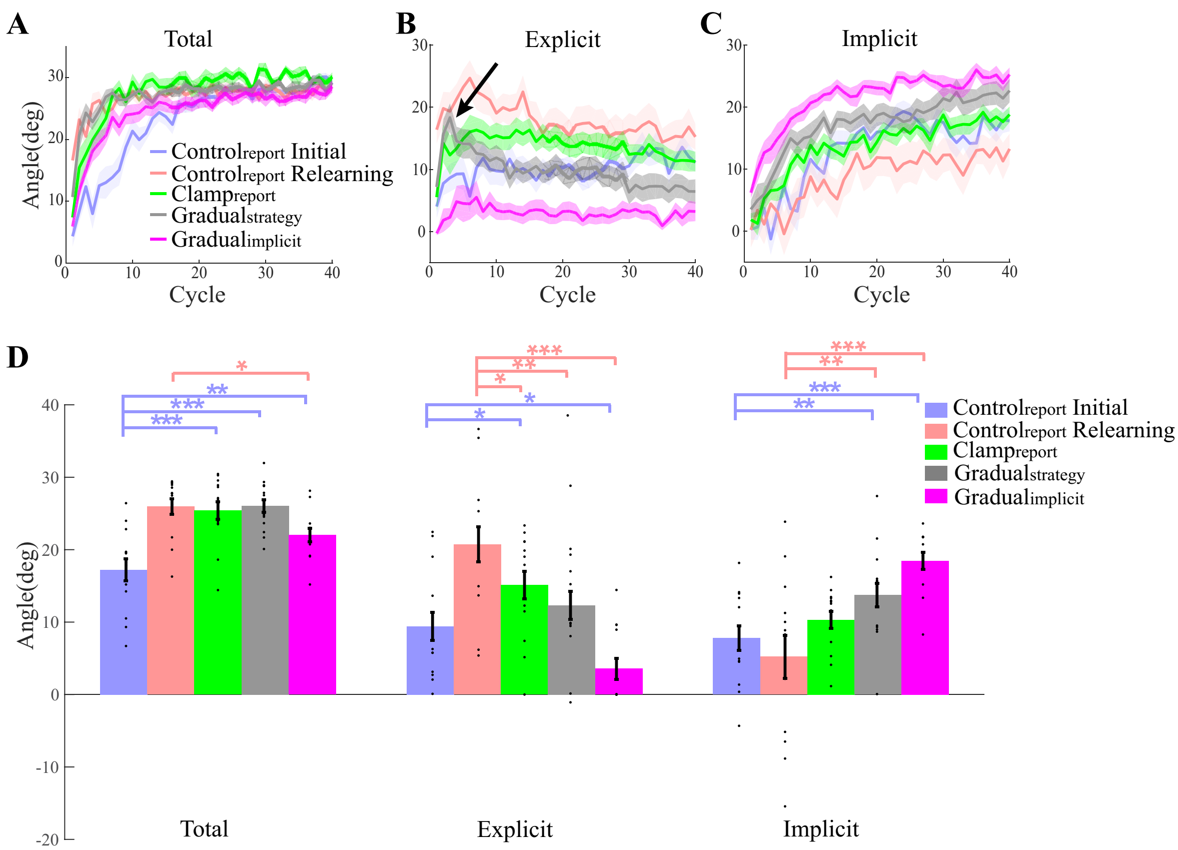

Fig. 5. Comparison of total learning and its explicit and implicit components between different groups in *experiment 2*. Total learning (*A*), explicit (*B*), and implicit (*C*) learning of the Clamp$_{report}$ Group, Gradual$_{strategy}$ Group, and Gradual$_{implicit}$ Group plotted with the two learning curves from the Control$_{report}$ Group. The black arrow in *B* points to the 2nd and 3rd cycles, which show substantial explicit learning. The shaded areas denote means ± SE *D*: learning rates are compared between groups. Each dot represents a participant. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

an arrow). For the 2nd and 3rd cycle, the Gradual$_{strategy}$ Group showed larger explicit learning when compared with the Control$_{report}$ Group's initial learning [15.64 ± 2.45° vs. 7.73 ± 1.98°, independent *t* test, $t_{(28)} = 2.51$, $P = 0.02$]. In fact, they did not differ from the Control$_{report}$ Group's relearning [$t_{(28)} = 1.13$, $P = 0.27$, $B = 0.56$]. However, this increase in explicit learning was only temporary, and it gradually decreased in the following cycles, suggesting that these participants did not continue to rely on strategic learning after its brief recall. At the end of the relearning phase, their implicit learning amounted to 22.11 ± 1.84, a 76.66% percentage of total learning, which was significantly larger than that of the Control$_{report}$ Group [$t_{(28)} = 3.04$, $P = 0.011$]. These results suggest that the saving effect shown by the Gradual$_{strategy}$ Group was mainly driven by implicit learning, although a brief recall of strategic learning was observed. A similar reliance on implicit learning was also present in the Gradual$_{implicit}$ Group: their average explicit learning at the end of the relearning (the last five cycles) was merely 2.81 ± 1.32°, but their average implicit learning was 24.80 ± 1.21°. Thus, after the Gradual$_{implicit}$ Group implicitly learned the gradually imposed rotation, and their subsequent savings were accompanied by substantially faster implicit learning.

In contrast to *experiment 1*, adaptation to gradual perturbations started to lead to savings in *experiment 2*. The critical change from *experiment 1* was that the participants were required to report their aiming directions (Fig. 6). During the initial learning phase, we found that the Gradual$_{strategy}$ Group countered the gradual perturbations better than the Gradual$_{implicit}$ Group and the Gradual Group from *experiment 1* in the last 10 cycles (data not shown). The latter two groups did not differ, suggesting that participants in *experiment 1* appear to learn implicitly when not required to report aiming. With aiming reports, some of the participants would develop an aiming strategy, and more closely follow the gradual perturbation than other participants without aiming strategy. Despite these group differences, error experienced by all three groups were quite small: the average error during initial learning was 3.99 ± 0.33°, 2.19 ± 0.23°, and 3.40 ± 0.43° for the Gradual, Gradual$_{strategy}$, and Gradual$_{implicit}$ Groups, respectively. In Fig. 6, we summarize possible key differences between groups who underwent gradual adaptation. The gradual adaptation was previously viewed as implicit learning with small sensory prediction errors. The setting of verbal reports of aiming presents participants extra visual landmarks (including tick marks and numbers) around the target when the reaching end point feedback is simultaneously shown. While the two groups with aiming reports showed robust savings, the Gradual$_{strategy}$ Group briefly recalled the explicit strategy during relearning, although their overall explicit learning did not differ from the control group. In contrast, the Gradual$_{implicit}$ Group did not show any strategy during the initial learning; their explicit learning remained small throughout the relearning phase. The explicit learning contributed more for the

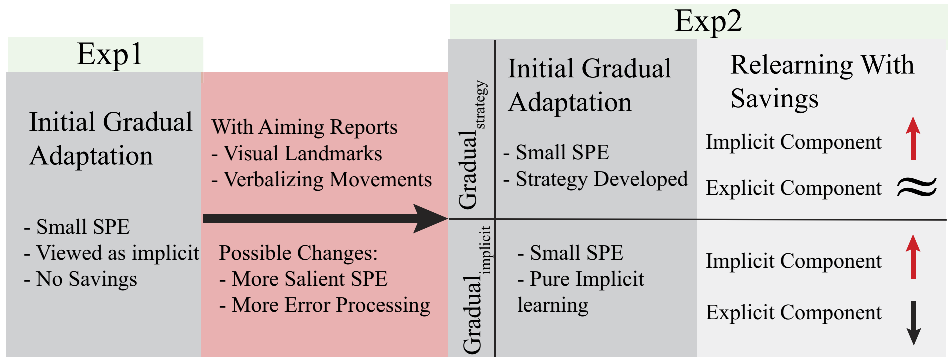

Fig. 6. A schematic illustration of the differences between gradual-learning groups from *experiments 1* and *2*. Gradual adaptation is traditionally regarded as implicit learning driven by small sensory prediction error (SPE), resulting in a lack of savings (*experiment 1*). The aiming reports used in *experiment 2* is accompanied by additional visual landmarks and the need to verbalize movement direction, possibly resulting in enhanced error saliency and error processing, despite that the SPE remains small. With these changes during the gradual adaptation, the $\text{Gradual}_{\text{strategy}}$ Group develops their aiming strategy, but the $\text{Gradual}_{\text{implicit}}$ Group fails to do so, but continues to rely on implicit learning. Both groups show savings that are primarily driven by increased implicit learning, although their explicit learning differs. During relearning, the $\text{Gradual}_{\text{implicit}}$ Group exhibits reduced explicit learning, while the $\text{Gradual}_{\text{strategy}}$ Group exhibits comparable explicit learning as the $\text{Control}_{\text{report}}$ Group.

$\text{Gradual}_{\text{strategy}}$ Group than for the $\text{Gradual}_{\text{implicit}}$ Group [$t_{(26)} = 3.51$, $P = 0.002$], and the implicit component contributed more to the $\text{Gradual}_{\text{implicit}}$ Group than to the $\text{Gradual}_{\text{strategy}}$ Group [$t_{(26)} = 2.27$, $P = 0.03$].

DISCUSSION

Understanding what is acquired and retained in memory is critical for cognitive neuroscience. Our study provides supporting evidence that savings for sensorimotor adaptation is independent of forming or recalling an explicit movement strategy. First, forming an explicit strategy during initial learning is not a prerequisite for savings since Clamp Groups (*experiments 1* and *2*) only implicitly learned from sensory prediction errors but still showed robust savings in delayed tests. Second, quick recall or formation of an explicit strategy during relearning is not necessary for savings since faster relearning in the $\text{Gradual}_{\text{report}}$ Group (*experiment 2*) is mainly driven by enhanced implicit learning during relearning, independent from whether an explicit strategy is formed during initial learning (as shown by both $\text{Gradual}_{\text{strategy}}$ and $\text{Gradual}_{\text{implicit}}$ Groups). These findings are at odds with the predictions of the explicit strategy account of savings, which attributes the faster relearning rate to a quick recall of adaptation strategy only, and further suggest that sensorimotor adaptation involves a dynamic interplay between implicit and explicit learning that is contingent on the specifics of learning protocol and available sensory feedback.

Savings without strategic learning. The error sensitivity account (Herzfeld et al. 2014) and the explicit strategy account (Morehead et al. 2015) differ by the necessary conditions for savings to occur. The former emphasizes the importance of experiencing similar sensory prediction errors (see also Leow et al. 2016), while the latter stresses the importance of forming an aiming strategy during initial learning. However, forming an explicit strategy requires large perturbations and salient errors (Morehead et al. 2015; Redding and Wallace 1993; Taylor et al. 2014). This is why the common paradigm to study savings is to abruptly introduce a large perturbation and sustain it over subsequent trials when people can generate an aiming strategy. On the other hand, if the perturbation size is small (Bond and Taylor 2015; Morehead et al. 2015; Taylor et al. 2014) or gradually introduced (Herzfeld et al. 2014; Werner et al. 2014), explicit learning, if there is any, will only constitute a small proportion of the total learning. The dependence on large and abrupt perturbations creates a dilemma: people inevitably develop an explicit strategy and experience salient errors simultaneously, rendering the isolation of their contributions to savings impossible. Interestingly, for other motor learning paradigms, such as sequence learning, explicit learning and implicit learning can be readily differentiated by task instruction, and their specific neural correlates could then be examined (Sami et al. 2014). However, the same instruction manipulation is not applicable to sensorimotor adaptation since, even without explicit instruction, people still develop an explicit strategy as long as the errors are salient (Huberdeau et al. 2015).

Using the task-irrelevant clamped feedback, we circumvents this methodological constraint. The clamped feedback has been shown to induce implicit learning of sensory prediction error, which is critical for sensorimotor adaptation (Morehead et al. 2017). As the participants are instructed to ignore the clamped feedback that is angularly offset from the target direction, they do not develop an explicit aiming strategy for visuomotor rotation. Their hand gradually deviates from the intended target direction without their awareness, indicating an implicit, sensory prediction error-driven learning. Importantly, while strategic learning is not observed during initial learning, the saving effect manifests itself when an abrupt perturbation is introduced during readaptation. Therefore, results from the Clamp Group indicate that forming an explicit strategy a priori is not a prerequisite for savings.

Aiming reports in *experiment 2* revealed that the participants developed an explicit strategy faster than the $\text{Control}_{\text{report}}$ Group during relearning. Why is strategic learning enhanced after error clamp learning? Error clamp learning requires the participants to ignore the task-irrelevant cursor and, thus, prevents forming strategic reaiming to correct for sensory prediction error. Hence, by instruction and by viewing the clamped feedback, the participant can learn that the cursor can be angularly rotated from their movement direction. This is a cognitive concept that is not immediately expressible in movements during error clamp learning, which is dominated by implicit learning. This kind of conceptual learning, though not manifested during initial learning, is possible to benefit future adaptation to visual perturbations that share the same conceptual structure, i.e., rotated visual representation of movements. The idea of conceptual learning has been shown in the realm of perceptual learning. For example, orientation discrimination of luminance gratings, initially encoded in V1, and orientation discrimination of bilaterally symmetric dot patterns, encoded in the higher visual cortex, can be completely transferred between each other (Wang et al. 2016). This stimulus-invariant learning transfer suggests that perceptual learning of discriminating elemental visual features involves learning on the conceptual level, e.g., acquiring abstract rules of orientation discrimination from simple visual features (Maniglia and Seitz 2018; Wang et al. 2016). We postulate that similar conceptual learning occurs in the error clamp learning since the clamped cursor feedback carries the rules of rotated visuomotor representation. If this is the case, the observed implicit learning during clamped feedback did not directly contribute to savings. Instead, people learned the rule of visuomotor rotation without immediate behavioral expression, and the learned rule enabled the fast formation of strategic reaiming in the relearning phase. Note, the conceptual learning here is different from strategic reaiming: the former is learned without immediate behavioral measures, while the latter is readily probed by verbal reports. If conceptual learning enables savings, then implicit learning during clamped feedback would not be the direct contributor to savings.

The results from the Gradual$_{report}$ Groups in *experiment 2* indicate the essential role of implicit learning for savings, particularly in the relearning phase. First, the Gradual Group without aiming report in *experiment 1* did not show any savings, replicating early findings (Herzfeld et al. 2014). The gradually introduced visuomotor rotation has been suggested to prevent the formation of explicit strategy (Codol et al. 2018), but this has not been tested directly. Our *experiment 2* showed that gradual adaptation could elicit strategic learning among some participants, since 16 out of 28 participants (Gradual$_{strategy}$ Group) generated explicit reaiming strategy during gradual adaptation, although their reported aiming offset was small (<5° on average). The Gradual$_{implicit}$ Group consisted of the other 12 participants, did not generate a reaiming strategy and were probably unaware of the gradually introduced perturbation. Importantly, no matter whether they generated an explicit strategy initially, both groups showed savings after gradual adaptation. The Gradual$_{strategy}$ Group showed a sign of recalling their strategy, mostly in the second and third cycles during readaptation, but their saving effect was still mostly caused by enhanced implicit learning. Interestingly, the Gradual$_{implicit}$ Group yielded faster relearning based on faster implicit learning, while their explicit learning remained significantly smaller than that of the Control Group. In fact, their explicit learning remained small throughout the readaptation phase, indicating that the development of the explicit strategy was affected by previous adaptation to gradual perturbations. Hence, on the basis of findings from *experiments 1* and *2*, we can conclude that neither acquiring an explicit strategy during initial learning nor a rapid recall/formation of it during readaptation is necessary.

Our findings also deviate from the predictions of the original error-sensitivity account. First, the error-sensitivity account emphasizes that the memory of similar errors leads to enhanced error responsivity for later learning (Herzfeld et al. 2014). Our results with clamped feedback, if not purely caused by conceptual learning, appear to suggest that experiencing sensory prediction errors facilitates subsequent strategic learning. Second, previous research emphasized that the errors during initial adaptation should be similar in terms of signs and magnitudes to those experienced during readaptation (Herzfeld et al. 2014; Leow et al. 2016). However, our participants did not experience similar errors during the gradual learning as during the readaptation phase: their performance error and sensory prediction error remained small (~3°) during initial learning. Once the gradual adaptation was coupled with aiming reports, the exposure of these small errors was still able to elicit a robust saving effect. Thus, similar performance error or sensory prediction error is not necessary for savings to occur. Recent research on so-called structural learning in motor adaptation have also provided supporting evidence for this conclusion: researchers have found that exposing people to the visuomotor rotation of random sizes and directions led to faster subsequent adaptation to abrupt rotation perturbations (Bond and Taylor 2017; Braun et al. 2009; Turnham et al. 2012). Among these studies, the random rotations experienced during initial learning also differed from the abrupt rotation experienced during relearning in both sign and magnitudes (Bond and Taylor 2017; Turnham et al. 2012). Thus, exposure to similar errors is not necessary for inducing savings, contradictory to the original error-sensitivity account (Herzfeld et al. 2014), as well as related computation models (Takiyama et al. 2015).

It is noteworthy that recent studies also examined whether structural learning is implicit or explicit. One study reported that extensive practice with perturbations changes involuntary visuomotor reflexes, suggesting that implicit learning constitutes an important part of structure learning of motor adaptation (Kobak and Mehring 2012). Nevertheless, a study on visuomotor rotation has found that the saving effect from structural learning is mainly expressed via explicit reaiming (Bond and Taylor 2017). Thus, both implicit and explicit learning might support structural learning and its related saving effect; their relative contributions might critically depend on the specifics of the learning session.

Error saliency plays an important role in inducing savings. Without forming or recalling an explicit strategy, how should we explain the saving effect enabled by clamped feedback and gradual adaptation? We propose that exposure to salient sensory prediction errors might be a common cause for the saving effect observed in different conditions. Previous studies distinguished implicit and explicit learning by checking whether people are aware of perturbations, or by related error signals where implicit learning and explicit learning are argued to rely on sensory prediction error and performance error, respectively (Taylor and Ivry 2011, 2014). For visuomotor rotation adaptation, in particular, the sensory prediction error is defined as the angular difference between the aiming direction and the end point feedback direction, and performance error is defined as the angular difference between the target and the hand-controlled cursor. In our experiment, error-clamp learning involves a cursor moving with an angular offset from the intended movement direction, and theoretically, this leads to a consistent 30° sensory prediction error but no performance error since no hand-controlled cursor is presented. Thus, large persistent sensory prediction error and a lack of observable strategic learning characterize the clamp learning. On the other hand, gradual learning involves trial-by-trial adaptation to gradually increasing rotations. Participants' intended movement direction slightly lags behind the actual rotation of the cursor, resulting in small sensory prediction errors (Figs. 2 and 4). Although participants in the $\text{Gradual}_{\text{strategy}}$ Group developed an explicit strategy, they experienced the sensory prediction errors of similar magnitudes as those in the $\text{Gradual}_{\text{implicit}}$ Group without forming an explicit strategy. Thus, participants with gradual adaptation also experienced a large number of trials with sensory prediction errors, though the error magnitude was substantially smaller than 30°. Thus, exposure of sensory prediction error is the common denominator for initial learning, not only for the diverse learning conditions in the present study, but also for all the existing data sets in visuomotor rotation adaptation that support the saving effect (Haith et al. 2015; Herzfeld et al. 2014; Morehead et al. 2015).

In *experiment 2*, explicit reports of aiming direction enabled otherwise absent savings after gradual adaptation. This result is puzzling at first sight, given that previous research has found that explicit reports of aiming do not affect adaptation performance (Bond and Taylor 2017; Taylor et al. 2014). It is worth noting that our participants, with or without aiming reports, experienced similar performance errors and sensory prediction errors. We postulate that there are two major changes brought about by explicit reports of aiming, both leading to more elaborate processing of sensory prediction error (Fig. 6). First, in addition to typical terminal feedback of the cursor, the participants were presented with tick marks and numbers around the visual target for reports of the aiming direction (Fig. 1). These landmarks might serve as augmented feedback to enhance the saliency of sensory prediction errors. This postulation is substantiated by the finding that providing participants landmarks for aiming increases implicit learning, which depends on sensory prediction error (Taylor and Ivry 2011). Furthermore, increasing the error saliency was recently shown to enhance the generalization of savings. For visuomotor rotation adaptation, the generalization of savings diminishes as a function of the angular separation between the learned direction and the generalization direction (Jiang et al. 2018; Yin et al. 2016). However, if errors are made more obvious by asking participants to move in orthogonal as opposed to oblique directions, or by displaying additional visual cues (a plain line between the target and the starting position in an identical experimental setup as in the current study), the limited generalization of savings can be enhanced (Jiang et al. 2018). Second, verbal reports of aiming itself might promote the processing of sensory prediction error. To report the aiming direction in each trial, participants are expected to carefully evaluate the visual feedback provided at the end of the movement, potentially leading to more elaborate processing of sensory prediction error. Thus, we tend to attribute the savings enabled by verbal reports of aiming to improved error processing during initial learning.

The intriguing relationship between implicit and explicit learning. Researchers originally intuited that cerebellar patients would rely more on strategic learning for countering perturbations, given their cerebellar lesion and compromised implicit learning. However, this is not supported by empirical findings. Cerebellar patients were equally impaired when adapting to gradual perturbations, which invoke more implicit learning, and abrupt perturbations, which invoke more explicit learning (Gibo et al. 2013; Schlerf et al. 2013; Smith and Shadmehr 2005). More evidence comes from a recent study showing that for visuomotor rotation, cerebellar patients demonstrated profound deficits not only in implicit learning (e.g., reduced aftereffect) but also in forming the explicit strategy (Butcher et al. 2017). Their impairments in both types of learning cannot be explained by their excessively large motor variance (see also Schlerf et al. 2013). Although the impairment in strategic learning has been argued to imply a possible role of the cerebellum in forming an action-outcome association (Butcher et al. 2017), we postulate that cerebellar processing of sensory prediction error is related to, instead of independent from, forming explicit strategy. Thus, it is possible that the impairment in implicit learning might be the cause of impaired explicit learning.

In fact, previous behavioral studies also provide indirect evidence that implicit learning interacts with explicit learning during sensorimotor adaptation. As we noted before, strategic reaiming can be prevented if the preparation time for movement is sufficiently short, a behavioral hallmark that reaiming is, indeed, deliberate cognitive control (Haith et al. 2015). A recent study found that this time constraint can be alleviated after repetitively exposed to abruptly introduced rotation perturbations (Huberdeau et al. 2019). In other words, with sufficient practice, the explicit learning that supports savings becomes more automatic and implicit. This finding echoes with the tenet in skill learning that learning progresses from an early phase that is cognitively demanding to a late phase that is more automatic and less effortful (Fitts and Posner 1967; Kelly and Garavan 2005). These findings suggest that the contribution of implicit and explicit processes to sensorimotor learning constantly changes. Accordingly, our findings also suggest that the dichotomy between implicit and explicit learning does not fully capture the savings in sensorimotor adaptation, echoing the recent scrutinization about the intriguing relationship between procedural and declarative knowledge (Stanley and Krakauer 2013).

Our quantification of explicit learning relied on verbal reports of aiming, which might not be an unbiased measure of explicit learning. Using shortened preparation time to prevent strategic reaiming, Leow and colleagues recently found that the estimated implicit learning was larger than what was obtained from verbal reports (Leow et al. 2017). Similarly, de Brouwer and colleagues used eye fixations before reaching movements to probe strategic learning. Although the verbally reported aiming direction was found to closely match the fixation-estimated direction, the verbal report itself made more participants fixate the reaiming direction with a faster adaptation rate, suggesting more participants used reaiming strategy (de Brouwer et al. 2018). Thus, these two alternative approaches both indicated that verbal reports of aiming might overestimate the explicit learning despite the fact that they qualitatively match. If a similar overestimation of explicit learning exists for our data set, it will imply that the enhanced implicit learning in the two gradual learning groups is underestimated, further supporting that the observed savings is implicitly learning-based. Nevertheless, our finding that verbal reports of aiming enabled otherwise absent savings after gradual adaptation demands more scrutiny about possible biases in the method of verbal reporting.

Neural correlates of savings and the relative contribution of explicit and implicit learning. Neurophysiological studies on neural correlates of savings in sensorimotor adaptation have produced conflicting results. For example, a recent study has found that neural correlates of savings include areas related to cognitive processes, including striatal, parietal, and cingulate cortical areas (Ruitenberg et al. 2018). These authors, thus, conclude that the savings relies on cognitive strategies or explicit learning (see also Della-Maggiore et al. 2017). In contrast, another study has found that participants with higher resting-state functional connectivity among default mode network (DMN) regions show more savings for visuomotor rotation adaptation (Cassady et al. 2018). As connectivity of DMN is anticorrelated with brain regions that are involved in cognitive control, these authors reach an opposite conclusion that savings is related to the procedural stages of sensorimotor adaptation, which is facilitated by the resting-state connectivity of DMN.

However, all these neurophysiological studies examined savings by repetitively exposing participants to abruptly induced perturbations in different learning sessions, and this treatment will inevitably lead to large explicit learning during initial training and faster recall of explicit learning during later training. Thus, it is not surprising that neural correlates of savings include various regions that are associated with cognitive processes pertinent to explicit learning. As our findings show that with proper experimental treatment savings in sensorimotor adaptation can be obtained by increased explicit or implicit learning, the neural correlates of savings are likely to vary depending on specific of learning protocols and available feedback. Furthermore, the neurophysiological basis for the interaction between implicit and explicit learning is understudied. For instance, the cerebellum is conventionally emphasized as the neural substrate for sensory prediction error-based learning (e.g., Tseng et al. 2007), but it also has extensive direct connections with prefrontal cortex, the locus of cognitive control with an implied role in saving effect (Kelly and Strick 2003; Seidler et al. 2017), and posterior parietal cortex, the critical area for visuomotor transformation (Clower et al. 1996; Tanaka et al. 2009). Network-level analyses have highlighted the role of the cerebellum in the dynamic interplay of the cerebellar-thalamic-cortical network that supports the learning and retention of sensorimotor adaptation (Della-Maggiore et al. 2017; Mawase et al. 2017; Ruitenberg et al. 2018). Given that the cerebellum processes sensory prediction error and performance error at the same time, we postulate that it contributes to both implicit learning and strategic learning. In particular, strategic learning can be viewed as an improvement in action selection, and how the cerebellum affects action selection is still under debate and needs further studies (Taylor and Ivry 2014).

Conclusions. Beyond motor adaptation, savings often manifests itself as implicit learning for various learning systems, including classical (Medina et al. 2001) and operant conditioning (Lebrón et al. 2004), perceptual learning (Liu and Weinshall 2000), semantic learning (Ebbinghaus 1913), motor skill learning (Dayan and Cohen 2011), and motor adaptation (Kojima et al. 2004; Krakauer et al. 2005). Thus, without an explicit strategy or elaborate cognitive control, people can exhibit faster relearning for classical conditioning, operant conditioning, perceptual learning, and improvement in motor acuity. Especially for motor skill learning, humans also demonstrate a saving effect without verbal knowledge about how it is achieved, a phenomenon often referred to as warming up effect in skill acquisition (Schmidt and Lee 2005). In this light, verbally reporting an adaptation strategy to counter a simple perturbation, as for visuomotor rotation, could be considered as a special case among diverse learning phenomena. Here, we do not mean to argue that explicit strategy is not used for savings in sensorimotor adaptation. After all, it is indisputable that people develop an explicit strategy for countering visuomotor rotation when this perturbation is introduced abruptly, and they can quickly recall this strategy during readaptation when the same or similar perturbations are presented. However, our findings indicate that explicit strategy is not necessary for the long-term learning effect of sensorimotor adaptation. Implicit learning, based on salient sensory prediction error, and conceptual learning, based on systematic action-outcome association, can support savings.

GRANTS

This study was funded by grants from National Natural Science Foundation of China (31671168, 31622029, and 61533001) and Beijing Natural Science Foundation (5194024).

DISCLAIMERS

The funding bodies in itself had no role in the design of the study nor in the collection, analysis, and interpretation of data or in writing the article.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

C.Y. and K.W. conceived and designed research; C.Y. performed experiments; C.Y. analyzed data; C.Y. and K.W. interpreted results of experiments; C.Y. prepared figures; C.Y. drafted manuscript; C.Y. and K.W. edited and revised manuscript; C.Y. and K.W. approved final version of manuscript.

REFERENCES

Baddeley RJ, Ingram HA, Miall RC. System identification applied to a visuomotor task: near-optimal human performance in a noisy changing task. *J Neurosci* 23: 3066–3075, 2003. doi:10.1523/JNEUROSCI.23-07-03066.2003.

Bond KM, Taylor JA. Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *J Neurophysiol* 113: 3836–3849, 2015. doi:10.1152/jn.00009.2015.

Bond KM, Taylor JA. Structural learning in a visuomotor adaptation task is explicitly accessible. *eNeuro* 4: ENEURO.0122-0117.2017, 2017.

Braun DA, Aertsen A, Wolpert DM, Mehring C. Motor task variation induces structural learning. *Curr Biol* 19: 352–357, 2009. doi:10.1016/j.cub.2009.01.036.

Butcher PA, Ivry RB, Kuo S-H, Rydz D, Krakauer JW, Taylor JA. The cerebellum does more than sensory prediction error-based learning in sensorimotor adaptation tasks. *J Neurophysiol* 118: 1622–1636, 2017. doi:10.1152/jn.00451.2017.

Cassady K, Ruitenberg M, Koppelmans V, Reuter-Lorenz P, De Dios Y, Gadd N, Wood S, Riascos Castenada R, Kofman I, Bloomberg J, Mulavara A, Seidler R. Neural predictors of sensorimotor adaptation rate and savings. *Hum Brain Mapp* 39: 1516–1531, 2018. doi:10.1002/hbm.23924.

Clower DM, Hoffman JM, Votaw JR, Faber TL, Woods RP, Alexander GE. Role of posterior parietal cortex in the recalibration of visually guided reaching. *Nature* 383: 618–621, 1996. doi:10.1038/383618a0.

Codol O, Holland PJ, Galea JM. The relationship between reinforcement and explicit control during visuomotor adaptation. *Sci Rep* 8: 9121, 2018. doi:10.1038/s41598-018-27378-1.

Dayan E, Cohen LG. Neuroplasticity subserving motor skill learning. *Neuron* 72: 443–454, 2011. doi:10.1016/j.neuron.2011.10.008.

de Brouwer AJ, Albaghdadi M, Flanagan JR, Gallivan JP. Using gaze behavior to parcellate the explicit and implicit contributions to visuomotor learning. *J Neurophysiol* 120: 1602–1615, 2018. doi:10.1152/jn.00113.2018.

Della-Maggiore V, McIntosh AR. Time course of changes in brain activity and functional connectivity associated with long-term adaptation to a rotational transformation. *J Neurophysiol* 93: 2254–2262, 2005. doi:10.1152/jn.00984.2004.

Della-Maggiore V, Villalta JI, Kovacevic N, McIntosh AR. Functional evidence for memory stabilization in sensorimotor adaptation: a 24-h resting-state fMRI study. *Cereb Cortex* 27: 1748–1757, 2017. doi:10.1093/cercor/bhv289.

Ebbinghaus H. *Memory: A Contribution to Experimental Psychology*. New York: Teachers College Press, 1913.

Fernandez-Ruiz J, Wong W, Armstrong IT, Flanagan JR. Relation between reaction time and reach errors during visuomotor adaptation. *Behav Brain Res* 219: 8–14, 2011. doi:10.1016/j.bbr.2010.11.060.

Fitts PM, Posner MI. Human performance. *Prof Saf* 22: 376–377, 1967.

Galea JM, Mallia E, Rothwell J, Diedrichsen J. The dissociable effects of punishment and reward on motor learning. *Nat Neurosci* 18: 597–602, 2015. doi:10.1038/nn.3956.

Gibo TL, Criscimagna-Hemminger SE, Okamura AM, Bastian AJ. Cerebellar motor learning: are environment dynamics more important than error size? *J Neurophysiol* 110: 322–333, 2013. doi:10.1152/jn.00745.2012.

Hadjiosif A, Smith M. Savings is restricted to the temporally labile component of motor adaptation. *Transl Comp Motor Control* 409–419, 2013.

Haith AM, Huberdeau DM, Krakauer JW. The influence of movement preparation time on the expression of visuomotor learning and savings. *J Neurosci* 35: 5109–5117, 2015. doi:10.1523/JNEUROSCI.3869-14.2015.

Herzfeld DJ, Vaswani PA, Marko MK, Shadmehr R. A memory of errors in sensorimotor learning. *Science* 345: 1349–1353, 2014. doi:10.1126/science.1253138.

Huang VS, Haith A, Mazzoni P, Krakauer JW. Rethinking motor learning and savings in adaptation paradigms: model-free memory for successful actions combines with internal models. *Neuron* 70: 787–801, 2011. doi:10.1016/j.neuron.2011.04.012.

Huberdeau DM, Haith AM, Krakauer JW. Formation of a long-term memory for visuomotor adaptation following only a few trials of practice. *J Neurophysiol* 114: 969–977, 2015. doi:10.1152/jn.00369.2015.

Huberdeau DM, Krakauer JW, Haith AM. Practice induces a qualitative change in the memory representation for visuomotor learning. *J Neurophysiol* 122: 1050–1059, 2019. doi:10.1152/jn.00830.2018.

Izawa J, Criscimagna-Hemminger SE, Shadmehr R. Cerebellar contributions to reach adaptation and learning sensory consequences of action. *J Neurosci* 32: 4230–4239, 2012. doi:10.1523/JNEUROSCI.6353-11.2012.

Izawa J, Shadmehr R. Learning from sensory and reward prediction errors during motor adaptation. *PLOS Comput Biol* 7: e1002012, 2011. doi:10.1371/journal.pcbi.1002012.

Jiang W, Yuan X, Yin C, Wei K. Visuomotor learning is dependent on direction-specific error saliency. *J Neurophysiol* 120: 162–170, 2018. doi:10.1152/jn.00787.2017.

Kelly AMC, Garavan H. Human functional neuroimaging of brain changes associated with practice. *Cereb Cortex* 15: 1089–1102, 2005. doi:10.1093/cercor/bhi005.

Kelly RM, Strick PL. Cerebellar loops with motor cortex and prefrontal cortex of a nonhuman primate. *J Neurosci* 23: 8432–8444, 2003. doi:10.1523/JNEUROSCI.23-23-08432.2003.

Kobak D, Mehring C. Adaptation paths to novel motor tasks are shaped by prior structure learning. *J Neurosci* 32: 9898–9908, 2012. doi:10.1523/JNEUROSCI.0958-12.2012.

Kojima Y, Iwamoto Y, Yoshida K. Memory of learning facilitates saccadic adaptation in the monkey. *J Neurosci* 24: 7531–7539, 2004. doi:10.1523/JNEUROSCI.1741-04.2004.

Krakauer JW, Ghez C, Ghilardi MF. Adaptation to visuomotor transformations: consolidation, interference, and forgetting. *J Neurosci* 25: 473–478, 2005. doi:10.1523/JNEUROSCI.4218-04.2005.

Krakauer JW, Ghilardi MF, Ghez C. Independent learning of internal models for kinematic and dynamic control of reaching. *Nat Neurosci* 2: 1026–1031, 1999. doi:10.1038/14826.

Krakauer JW, Pine ZM, Ghilardi M-F, Ghez C. Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J Neurosci* 20: 8916–8924, 2000. doi:10.1523/JNEUROSCI.20-23-08916.2000.

Lackner JR, Dizio P. Rapid adaptation to Coriolis force perturbations of arm trajectory. *J Neurophysiol* 72: 299–313, 1994. doi:10.1152/jn.1994.72.1.299.

Landi SM, Baguear F, Della-Maggiore V. One week of motor adaptation induces structural changes in primary motor cortex that predict long-term memory one year later. *J Neurosci* 31: 11808–11813, 2011. doi:10.1523/JNEUROSCI.2253-11.2011.

Lebrón K, Milad MR, Quirk GJ. Delayed recall of fear extinction in rats with lesions of ventral medial prefrontal cortex. *Learn Mem* 11: 544–548, 2004. doi:10.1101/lm.78604.

Leow LA, de Rugy A, Marinovic W, Riek S, Carroll TJ. Savings for visuomotor adaptation require prior history of error, not prior repetition of successful actions. *J Neurophysiol* 116: 1603–1614, 2016. doi:10.1152/jn.01055.2015.

Leow L-A, Gunn R, Marinovic W, Carroll TJ. Estimating the implicit component of visuomotor rotation learning by constraining movement preparation time. *J Neurophysiol* 118: 666–676, 2017. doi:10.1152/jn.00834.2016.

Liu Z, Weinshall D. Mechanisms of generalization in perceptual learning. *Vision Res* 40: 97–109, 2000. doi:10.1016/S0042-6989(99)00140-6.

Miall RC, Wolpert DM. Forward models for physiological motor control. *Neural Netw* 9: 1265–1279, 1996. doi:10.1016/S0893-6080(96)00035-4.

Maniglia M, Seitz AR. Towards a whole brain model of perceptual learning. *Curr Opin Behav Sci* 20: 47–55, 2018. doi:10.1016/j.cobeha.2017.10.004.

Mawase F, Bar-Haim S, Shmuelof L. Formation of long-term locomotor memories is associated with functional connectivity changes in the cerebellar-thalamic-cortical network. *J Neurosci* 37: 349–361, 2017. doi:10.1523/JNEUROSCI.2733-16.2016.

Mazzoni P, Krakauer JW. An implicit plan overrides an explicit strategy during visuomotor adaptation. *J Neurosci* 26: 3642–3645, 2006. doi:10.1523/JNEUROSCI.5317-05.2006.

Medina JF, Garcia KS, Mauk MD. A mechanism for savings in the cerebellum. *J Neurosci* 21: 4081–4089, 2001. doi:10.1523/JNEUROSCI.21-11-04081.2001.

Morehead JR, Qasim SE, Crossley MJ, Ivry R. Savings upon re-aiming in visuomotor adaptation. *J Neurosci* 35: 14386–14396, 2015. doi:10.1523/JNEUROSCI.1046-15.2015.

Morehead JR, Taylor JA, Parvin DE, Ivry RB. Characteristics of implicit sensorimotor adaptation revealed by task-irrelevant clamped feedback. *J Cogn Neurosci* 29: 1061–1074, 2017. doi:10.1162/jocn_a_01108.

Morey RD, Wagenmakers E-J. Simple relation between Bayesian order-restricted and point-null hypothesis tests. *Stat Probab Lett* 92: 121–124, 2014. doi:10.1016/j.spl.2014.05.010.

Morton SM, Bastian AJ. Cerebellar contributions to locomotor adaptations during splitbelt treadmill walking. *J Neurosci* 26: 9107–9116, 2006. doi:10.1523/JNEUROSCI.2622-06.2006.

Redding GM, Wallace B. Adaptive coordination and alignment of eye and hand. *J Mot Behav* 25: 75–88, 1993. doi:10.1080/00222895.1993.9941642.

Ruitenberg MFL, Koppelmans V, De Dios YE, Gadd NE, Wood SJ, Reuter-Lorenz PA, Kofman I, Bloomberg JJ, Mulavara AP, Seidler RD. Neural correlates of multi-day learning and savings in sensorimotor adaptation. *Sci Rep* 8: 14286, 2018. doi:10.1038/s41598-018-32689-4.

Sami S, Robertson EM, Miall RC. The time course of task-specific memory consolidation effects in resting state networks. *J Neurosci* 34: 3982–3992, 2014. doi:10.1523/JNEUROSCI.4341-13.2014.

Schlerf JE, Xu J, Klemfuss NM, Griffiths TL, Ivry RB. Individuals with cerebellar degeneration show similar adaptation deficits with large and small visuomotor errors. *J Neurophysiol* 109: 1164–1173, 2013. doi:10.1152/jn.00654.2011.

Schmidt RA, Lee TD. *Motor Control and Learning: A Behavioral Emphasis*. Champaign, IL: Human Kinetics, 2005.

Seidler RD, Gluskin BS, Greeley B. Right prefrontal cortex transcranial direct current stimulation enhances multi-day savings in sensorimotor adaptation. *J Neurophysiol* 117: 429–435, 2017. doi:10.1152/jn.00563.2016.

Shadmehr R, Mussa-Ivaldi FA. Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14: 3208–3224, 1994. doi:10.1523/JNEUROSCI.14-05-03208.1994.

Smith MA, Shadmehr R. Intact ability to learn internal models of arm dynamics in Huntington's disease but not cerebellar degeneration. *J Neurophysiol* 93: 2809–2821, 2005. doi:10.1152/jn.00943.2004.

Stanley J, Krakauer JW. Motor skill depends on knowledge of facts. *Front Hum Neurosci* 7: 503, 2013. doi:10.3389/fnhum.2013.00503.

Synofzik M, Lindner A, Thier P. The cerebellum updates predictions about the visual consequences of one's behavior. *Curr Biol* 18: 814–818, 2008. doi:10.1016/j.cub.2008.04.071.

Takiyama K, Hirashima M, Nozaki D. Prospective errors determine motor learning. *Nat Commun* 6: 5925, 2015. doi:10.1038/ncomms6925.

Tanaka H, Sejnowski TJ, Krakauer JW. Adaptation to visuomotor rotation through interaction between posterior parietal and motor cortical areas. *J Neurophysiol* 102: 2921–2932, 2009. doi:10.1152/jn.90834.2008.

Taylor JA, Ivry RB. Flexible cognitive strategies during motor learning. *PLOS Comput Biol* 7: e1001096, 2011. doi:10.1371/journal.pcbi.1001096.

Taylor JA, Ivry RB. Cerebellar and prefrontal cortex contributions to adaptation, strategies, and reinforcement learning. *Prog Brain Res* 210: 217–253, 2014. doi:10.1016/B978-0-444-63356-9.00009-1.

Taylor JA, Klemfuss NM, Ivry RB. An explicit strategy prevails when the cerebellum fails to compute movement errors. *Cerebellum* 9: 580–586, 2010. doi:10.1007/s12311-010-0201-x.

Taylor JA, Krakauer JW, Ivry RB. Explicit and implicit contributions to learning in a sensorimotor adaptation task. *J Neurosci* 34: 3023–3032, 2014. doi:10.1523/JNEUROSCI.3619-13.2014.

Tseng YW, Diedrichsen J, Krakauer JW, Shadmehr R, Bastian AJ. Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *J Neurophysiol* 98: 54–62, 2007. doi:10.1152/jn.00266.2007.

Turnham EJ, Braun DA, Wolpert DM. Facilitation of learning induced by both random and gradual visuomotor task variation. *J Neurophysiol* 107: 1111–1122, 2012. doi:10.1152/jn.00635.2011.

Wang R, Wang J, Zhang J-Y, Xie X-Y, Yang Y-X, Luo S-H, Yu C, Li W. Perceptual learning at a conceptual level. *J Neurosci* 36: 2238–2246, 2016. doi:10.1523/JNEUROSCI.2732-15.2016.

Werner S, Schorn CF, Bock O, Theysohn N, Timmann D. Neural correlates of adaptation to gradual and to sudden visuomotor distortions in humans. *Exp Brain Res* 232: 1145–1156, 2014. doi:10.1007/s00221-014-3824-1.

Yin C, Bi Y, Yu C, Wei K. Eliminating direction specificity in visuomotor learning. *J Neurosci* 36: 3839–3847, 2016. doi:10.1523/JNEUROSCI.2712-15.2016.

Zarahn E, Weston GD, Liang J, Mazzoni P, Krakauer JW. Explaining savings for visuomotor adaptation: linear time-invariant state-space models are not sufficient. *J Neurophysiol* 100: 2537–2548, 2008. doi:10.1152/jn.90529.2008.