

RESEARCH ARTICLE

Control of Movement

Sensorimotor knowledge from task-irrelevant feedback contributes to motor learning

Yajie Liu,^{1*} Wanying Jiang,^{1,3*} Yuqing Bi,¹ and Kunlin Wei^{1,2,3}

¹School of Psychological and Cognitive Sciences, Peking University, Beijing, China; ²Beijing Key Laboratory of Behavior and Mental Health, Beijing, China; and ³Peking-Tsinghua Center for Life Sciences, Beijing, China

Abstract

Exposure to task-irrelevant feedback leads to perceptual learning, but its effect on motor learning has been understudied. Here, we asked human participants to reach a visual target with a hand-controlled cursor while observing another cursor moving independently in a different direction. Although the task-irrelevant feedback did not change the main task's performance, it elicited robust savings in subsequent adaptation to classical visuomotor rotation perturbation. We demonstrated that the saving effect resulted from a faster formation of strategic learning through a series of experiments, not from gains in the implicit learning process. Furthermore, the saving effect was robust against drastic changes in stimulus features (i.e., rotation size or direction) or task types (i.e., for motor adaptation and skill learning). However, the effect was absent when the task-irrelevant feedback did not carry the visuomotor relationship embedded in visuomotor rotation. Thus, though previous research on perceptual learning has related task-irrelevant feedback to changes in early sensory processes, our findings support its role in acquiring abstract sensorimotor knowledge during motor learning. Motor learning studies have traditionally focused on task-relevant feedback, but our study extends the scope of feedback processes and sheds new light on the dichotomy of explicit and implicit learning in motor adaptation and motor structure learning.

NEW & NOTEWORTHY When the motor system faces perturbations, such as fatigue or new environmental changes, it adapts to these changes by voluntarily selecting new action plans or implicitly fine-tuning the control. We show that the action selection part can be enhanced without practice or explicit instruction. We further demonstrate that this enhancement is probably linked to the acquisition of abstract knowledge about the to-be-adapted novel visual feedback. Our findings draw an interesting parallel between motor and perceptual learning by showing that top-down information affects both types of procedural learning.

implicit learning; knowledge; motor adaptation; procedural knowledge; task-irrelevant feedback

INTRODUCTION

Learning by doing is the first tenet of motor learning (1, 2). Motor learning can be roughly categorized as skill acquisition, e.g., acquiring a novel motor skill such as playing tennis, and motor adaptation, i.e., recalibrating the motor system to counter perturbations in the body and from the environment (3, 4). Both types of motor learning require the deliberate practice of the task. Besides the repeated practice of the actions, skill acquisition undisputedly necessitates learning the task's knowledge, e.g., the game setting of tennis, physical properties of the tennis racket, and the ball (5).

On the other hand, motor adaptation was traditionally viewed as an implicit and automatic recalibration of the motor system to counter the disturbances of the bodily state (e.g., fatiguing muscles) or from the external environment (e.g., weight changes of the handheld teacup). In recent years, researchers have found that motor adaptation also involves intentional learning, especially strategic learning of movement solutions (6). Thus, deliberate practice of actions and motor knowledge acquisition support both motor adaptation and motor skill acquisition.

However, perceptual learning studies have shown that passive stimulation, i.e., exposing the observers to sensory

* Y. Liu and W. Jiang contributed equally to this work.

Correspondence: K. Wei (wei.kunlin@pku.edu.cn).

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stimuli without requiring them to attend to the stimulation actively, can lead to a robust learning effect (7). In other words, perceptual improvement can be achieved without deliberate practice. In the so-called task-irrelevant feedback paradigm, for example, participants showed improvement in visual motion discrimination when moving dots were presented slightly below the detection threshold while they were occupied by the main task of visual detection of letters (8). The improvement in discriminating task-irrelevant stimuli, i.e., visual motion stimuli, thus occurs without deliberate practice or even attention (9, 10). This exposure-elicited learning has been linked to changes in early visual processing driven by internal reinforcement signals triggered by the main task processing (11). The same effect has also been shown in auditory perceptual learning (2).

To our best knowledge, studies of motor learning have not examined whether the motor system can incorporate task-irrelevant feedback and subsequently improve other motor tasks other than the main task at hand. Motor learning studies typically focus on task-relevant feedback and address theoretical questions including what sensory cues support superior motor performance during motor learning (12), how the motor system learns to efficiently and effectively extract sensory information relevant to the to-be-learned action (13), and how the motor system learns to better the combination of task-relevant variables and loosen the control of task-irrelevant variables (14, 15). The possibility that concurrent but task-irrelevant feedback can be learned by the motor system, similar to perceptual learning of task-irrelevant feedback, has been overlooked. Learning from task-irrelevant feedback without deliberate practice is different from similar but related motor-learning approaches such as observational learning, motor imagery practice, and coaching by verbal instruction. These approaches do not need to practice a motor task physically, but they all require the learner to emulate the to-be-learned actions with task-relevant feedback. Observational learning involves unconscious or intentional simulation of the observed actions (16–19). Motor imagery practice involves deliberate mental simulation of remembered actions (20). Verbal instruction delivers motor knowledge related to task fulfillment, e.g., action solutions or strategies, directly to the learner (21, 22). Thus, the verbal or nonverbal feedback in these approaches is task relevant, intentionally or implicitly processed by the learners for bettering their motor performance. Inspired by perceptual learning of irrelevant feedback, we propose that task-irrelevant feedback presented during an attended motor task can elicit performance improvement in a delayed test of another motor task. In particular, we figure that the spatiotemporal relationship between the task-irrelevant feedback and the simultaneous movement can be abstracted by the learner and used for subsequent actions.

Here, we use the classical visuomotor rotation (VMR) adaptation as a test bed for the benefit of learning from task-irrelevant feedback. Participants reach with a hand cursor while observing simultaneous, rotated visual feedback, which does not affect their reaching performance. The rotated but task-irrelevant feedback leads to savings in a delayed visuomotor rotation adaptation test. We show that this saving effect, a hallmark of the long-term memory of motor adaptation (23, 24), does not result from enhanced implicit learning but from

the faster formation of a strategic solution to counter perturbations. Further experiments on modifying the stimulus features (rotation size and direction in *experiments 1* and *2*, respectively) and the task types (motor adaptation vs. skill learning in *experiment 3*) provide supporting evidence that participants obtained conceptual visuomotor knowledge from the task-irrelevant feedback.

MATERIALS AND METHODS

Participants

A total of 72 right-handed participants (36 females, aged 21.0 ± 2.1 yr) were recruited in this study. The participants were randomly assigned to six experimental groups (12–14 people in each group). All participants had not known the purpose of the experiment or experienced visuomotor feedback manipulations that were used in the present study. All participants signed written informed consent before the experiment and received monetary compensation for their time after the experiment. Experimental procedures were approved by the Institutional Review Board of Peking University.

Apparatus

The participants completed the experiments in a quiet and dim-lighted room. They sat in a height-adjustable chair in front of the table, holding a stylus vertically with their right hand (Fig. 1A). The task required them to move the stylus horizontally on a digitizing tablet (Wacom PTK-1240). The movement of the stylus was measured with a sampling frequency of 200 Hz and a spatial resolution of 0.01 mm. The visual stimuli were presented on a vertically mounted monitor (Acer T232HL) in front of participants at eye level with a refresh rate of 60 Hz. A black paperboard is placed horizontally underneath the monitor, approximately at the participant's chest's height to occlude vision of the hand and arm. The actual hand movement and its visual representations on the monitor maintained a 1:1 correspondence ratio when visual perturbation was not applied.

Experimental Procedures

Our study included three experiments with similar procedures (Fig. 1B). Before each experiment, participants practiced a few unperturbed trials with or without the hand cursor to familiarize themselves with the experimental setup. All experiments shared the same five consecutive phases, i.e., baseline, initial learning, washout, relearning, and washout. They only differed by what the participant experienced during the initial learning phase.

Experiment 1: Learning from a Task-Irrelevant Cursor with Fixed Directions

The task required participants to make a single, rapid shooting movement from a center start position to one of the eight radially arranged targets. Each target was shown as a green hollow disk (3.9 mm in diameter) placed along a 10-cm-radius invisible circle with an angular separation of 45° . The movement goal was to quickly slide through the target as accurately as possible using the right hand or its hand cursor depend on the task settings. The hand cursor was

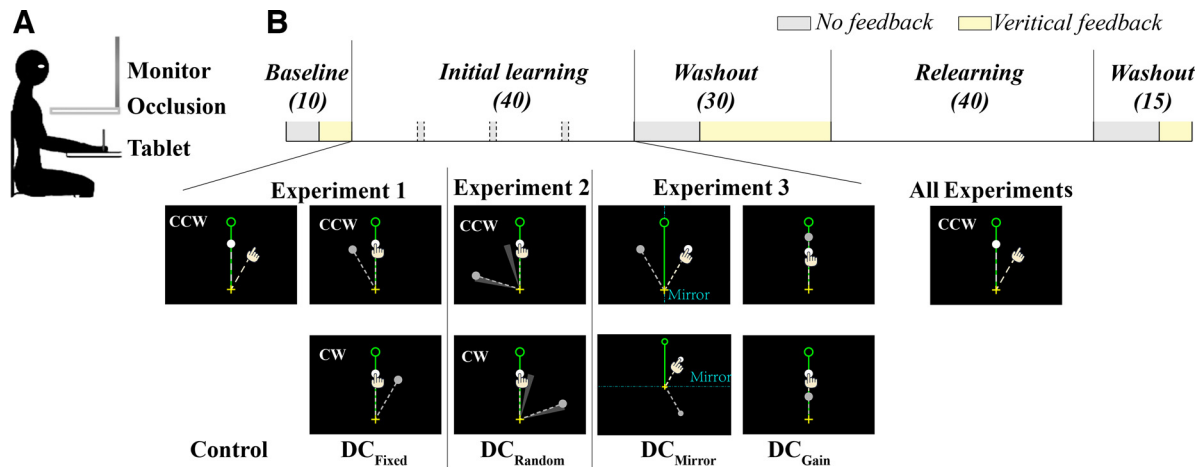


Figure 1. The experimental setup and procedures. *A*: a schematic of the experimental setup. *B*: the experimental procedures used in the three experiments. All participants went through the same series of phases except a distinct initial learning phase for each group. In the initial learning phase, the participants in the Control condition reached their hand toward the visual target while the only cursor on the screen, as their hand representation marked in white, was rotated 30° counterclockwise (CCW) from their actual movement. On the other hand, the participants in all experimental conditions moved toward the target, but their hand was shown as an unrotated, white cursor. However, they were also presented with a second cursor (marked in gray) that moved synchronously with the first cursor. Different experiments and conditions only varied in terms of the spatial relationship between the first and second cursor. For the DC_{Fixed} condition, the second cursor moved 30° clockwise (CW) or 30° CCW from the target direction, invariantly across trials. Two separate subgroups of participants experienced the fixed 30° CW or CCW. For the DC_{Random} condition, the second cursor moved with a different oblique direction each trial cycle, with an angle size randomly selected from (10°, 20°) and (70°, 80°). Two subgroups experienced the random angle either in the CW or CCW direction, respectively. For the DC_{Mirror} condition, the second cursor's movement mirrored the main cursor, either horizontally or vertically, for the two subgroups of participants. For the DC_{Gain} condition, the second cursor moved with an amplitude ratio varying randomly across trial cycles. One subgroup experienced an amplified visuomotor gain range of (1.2, 1.4), and the other subgroup a reduced gain range of (0.6, 0.8). Three no-feedback catch trial cycles were interspersed during initial learning to examine possible implicit adaptation. After a washout phase, the participants from all conditions adapted to the same 30° CCW visuomotor rotation to evaluate their possible learning during the initial learning phase. DC, dual cursor.

presented as a white disk (3.9 mm in diameter). At the beginning of each trial, the subjects placed their hand (i.e., the tip of the stylus) at the starting position, which was displayed as a yellow cross (4 mm per line). To facilitate the participant to return to the starting position without seeing their hand, we showed a white ring centered at the start position with a radius equal to the distance between the hand and the starting position. The ring, shown with a line width of 1.5 mm, was only visible within 25 mm around the starting position, and it contracted when the hand approached the starting point. Once the hand stayed at the starting point for 500 ms, the white ring disappeared, and one of the eight targets appeared. At the same time, a computer speaker sounded a beep to signal the participant to move immediately. The hand cursor was visible until the movement amplitude exceeded 10 cm when another beep sound was played to signify the end of the trial. If the participant successfully hit the target, the target would change from a green hollow disk to a solid green disk for 1 s, and the speaker would play a pleasant beep sound. We showed the cumulative number of successful hits in the upper right corner of the monitor to motivate the participant. The time when the hand moved 7 mm was regarded as the start time of the movement (25). The time interval between the target appearance and the movement start was regarded as reaction time. A warning sound was played, and the target was extinguished if the reaction time exceeded 1,500 ms; the participant was required to repeat the trial. The time interval between the start time and the time the hand exceeded the target distance was regarded as movement time. A low-pitched, unpleasant tone warned the participants when they

moved too slowly with a movement time larger than 375 ms, but they did not need to repeat the trial in this case.

In some trials, we used the aiming report paradigm to measure the amplitude of strategic learning (6). Before the movement, we displayed a ring of numbers around the green target with a 5° spacing in between. The target was also always labeled as 0, the clockwise (CW) directions were labeled with negative numbers, and the counterclockwise (CCW) directions with positive numbers. For example, 5° CCW from the target would be 1, and 5° CW would be -1. Before these trials, participants vocally reported a number to indicate where they aimed for their movement; thus, the aiming direction indicates the extent of explicit learning. The number was recorded by the experimenter for offline analysis.

As each target appeared randomly at the eight possible locations only once over eight consecutive trials, these eight trials constituted a trial cycle whose average performance was analyzed. Before the formal data collection, our participants familiarized themselves with the task and experimental setup by reaching the targets for three cycles. These familiarization trials showed the hand cursor without any perturbation. In the last cycle, the participants were also given a chance to practice the aiming report trials. In the subsequent baseline phase, participants completed movements without the hand cursor for five cycles and then with the veridical hand cursor for additional five cycles. The baseline phase was used to measure the directional bias for each target before learning. During the initial learning phase, the participants in the DC_{Fixed} condition (dual cursor, with a fixed movement direction) moved their hand cursor toward

the target, whereas a second cursor simultaneously moved 30° counterclockwise (CCW) or clockwise (CW) to the target direction. Two subgroups of participants ($n = 12$ each group) experienced the two directions separately. The hand cursor was still shown as a white cursor as in the baseline phase, but the “dual” cursor was shown as a gray disk (Fig. 1B). The task goal was still to slice the hand, shown as the white cursor throughout the experiment, through the target. The instruction for the initial learning phase was “Please ignore the unrelated gray cursor and slice the green target with the white cursor.” The second cursor was similar to the error-clamp cursor, which researchers have used extensively to induce implicit adaptation (27). However, as our participants could control their hand cursor to aim for the target, we expected that they would not deviate their hand, as in typical error-clamp learning. To examine whether the second task-irrelevant cursor induced implicit learning, we inserted three additional cycles of catch trials, which showed no cursor feedback at all. These catch cycles were inserted after the 10th, 20th, and 30th cycles during initial learning. Before the catch cycle, a text instruction was shown on the monitor to remind the participant to aim for the target directly and refrain from using any strategy. Implicit learning, if any, would emerge if the hand cursor was not shown. In this case, the hand would be biased in the opposite direction of the second cursor. We also recruited a Control group ($n = 12$) who controlled the hand cursor to make the shooting movement without the second cursor.

After the initial learning phase, all participants moved without the cursor feedback for 10 cycles and then with veridical feedback for additional 20 cycles to wash out any apparent effect of initial learning (28). In the subsequent relearning phase, our participants from all the conditions adapted to a conventional, abrupt visuomotor rotation (VMR) where the hand cursor was rotated 30° CCW and remained rotated for 40 cycles. No second cursor was shown in this phase since this phase aimed to evaluate whether the participants acquired sensorimotor knowledge of directional deviations in the initial learning phase to facilitate conventional VMR adaptation. In the relearning phase, we used the aiming report paradigm, as described before to measure explicit learning. The instruction for this relearning phase was “Please slice through the green target with the white cursor; orally report your aiming direction before starting the movement.” For the DC_{Fixed} condition, the aiming report was not used for initial learning as the participants were instructed explicitly to aim for the target with the hand cursor. The Control group gave aiming reports in both initial learning and relearning phases.

After the relearning phase, the participants in the DC_{Fixed} condition underwent another washout phase with 10 no-feedback cycles and 5 vertical-feedback cycles. The Control group only had five no-feedback washout cycles.

Experiment 2: Learning from a Task-Irrelevant Cursor with Random Directions

Experiment 2 aimed to examine whether motor knowledge can be obtained from a task-irrelevant dual cursor with a random rotation size. We recruited a new group of participants (the DC_{Random} condition, $n = 12$) to follow the same

procedure as in *experiment 1* except with a different dual cursor. For each trial in the initial learning phase, we drew the second cursor’s rotated angle from a uniform distribution spanning from 10° to 20° and 70° to 80°. Thus, these participants never experienced a 30° rotation that they were about to adapt to in the relearning phase. Furthermore, the average angle of these random rotations was 45°, different from 30°. Half of the participants experienced CW-rotated dual cursors and the other half the CCW ones.

Experiment 3: Learning from a Task-Irrelevant Cursor with or without Angular Manipulations

We hypothesized that the motor knowledge that facilitated rotation adaptation was a directional deviation of visuomotor representation. Given its abstract nature, participants shall obtain this knowledge from completely distinct motor learning tasks, as long as a visuomotor directional deviation is available as in VMR. Instead of presenting the second cursor as rotated from the main cursor, a new group of participants (the DC_{Mirror} condition, $n = 12$) experienced a mirror reversal representation, i.e., the second cursor moved in a mirror symmetry fashion as the hand cursor. Mirror reversal learning is regarded as skill learning as opposed to motor adaptation in which the VMR adaptation belongs to (29). We randomly assigned the participants into two subgroups: one experienced the second cursor mirroring the hand cursor along the left-right midline of the horizontal workspace, the other experienced the second cursor mirroring the front-back midline. We hypothesized that both subgroups should acquire directional deviation knowledge and exhibit savings in subsequent visuomotor rotation, despite a lack of visuomotor adaptation during initial learning. The instruction remained the same as in *experiment 1* with a rotated, second cursor: “Please ignore the unrelated gray cursor and slice the green target with the white cursor.”

We also predict that task-irrelevant feedback that lacks directional deviations would not lead to savings in visuomotor rotation. We used the classical visuomotor gain adaptation (30) as a test bed for this hypothesis: the second cursor followed the same direction (thus without direction manipulations) as the hand cursor but its movement amplitude was scaled by a ratio. We recruited a new group of participants (the DC_{Gain} condition, $n = 12$) to experience visuomotor gain changes. The gain changed from cycle to cycle. For each cycle, we drew the ratio randomly from a uniform distribution between 0.4 and 0.6 (gain-down) and between 1.2 and 1.4 (gain-up). Thus, one type of gain adaptation caused a cursor motion smaller than expected, whereas the other type of gain adaptation caused a cursor motion larger than expected. We randomly split the 12 participants into two subgroups who experienced gain-up and gain-down manipulation, respectively, during the initial learning phase. Though learning a novel visuomotor gain is regarded as motor adaptation, we hypothesize that it lacks the directional deviation of visuomotor representation and thus prevents forming relevant motor knowledge for VMR adaptation and savings. For both DC_{Mirror} and DC_{Gain} conditions, all procedures remained the same as in *experiment 1* except the new initial learning phase.

Data Analysis

The learning with VMR perturbations can be quantified by the angular deviation of the hand movement. The hand movement direction was from the starting position to the end point position. As our task required participants to shoot across the target, the intersection of the shooting movement and the invisible target arc was the end point position. Our results remain unchanged if the location at the time of peak velocity, instead of the end point location, was used to define the movement direction. The explicit learning was indicated by the aiming direction reported by the participant when applicable. The implicit learning was thus determined by subtracting the explicit learning from the total learning. The learning was shown as a rapid reduction of the hand's angular error from the target direction. We defined the learning rate as the average reduction within a window of initial trial cycles (31). The larger the reduction, the faster the learning rate. The window extended from the 2nd cycle to the 12th cycle, a fast-learning period where the average angular deviation over three successive cycles significantly differed from the previous three cycles (Fig. 2). The rate of explicit and implicit learning was also computed in the same window when applicable.

To assess whether the task-irrelevant cursor interfered with the shooting movement, we used independent *t* tests to

compare the hand directional deviation against zero during the exposure period and during the interspersed catch trials. As explicit learning appeared to be minimal in the first cycle of the relearning phase, we also used independent *t* tests to compare this cycle against zero. We examined the saving effect by comparing the learning rate in all experimental conditions with the control group's learning rate in the initial and relearning phases, respectively. If participants learned from the task-irrelevant feedback, their VMR learning rate would be faster than the Control group's initial learning but comparable to the Control group's relearning.

Besides quantifying the learning by using the angular deviation of the hand, we also computed the average reaction time (RT) and movement time (MT) to characterize the movement changes. We wanted to test the possibility that our participants emulate the reaiming strategy to counter the task-irrelevant cursor even though they might not show any observable hand deviation. That is, they might covertly simulate the reaiming strategy during the initial learning phase while still being able to achieve the target with the hand cursor. In this case, we would expect an increase in reaction time or movement time during the initial learning phase compared with the baseline phase. We thus compared the average RT and MT between the baseline phase (averaged over the 5 baseline cycles with the hand cursor only)

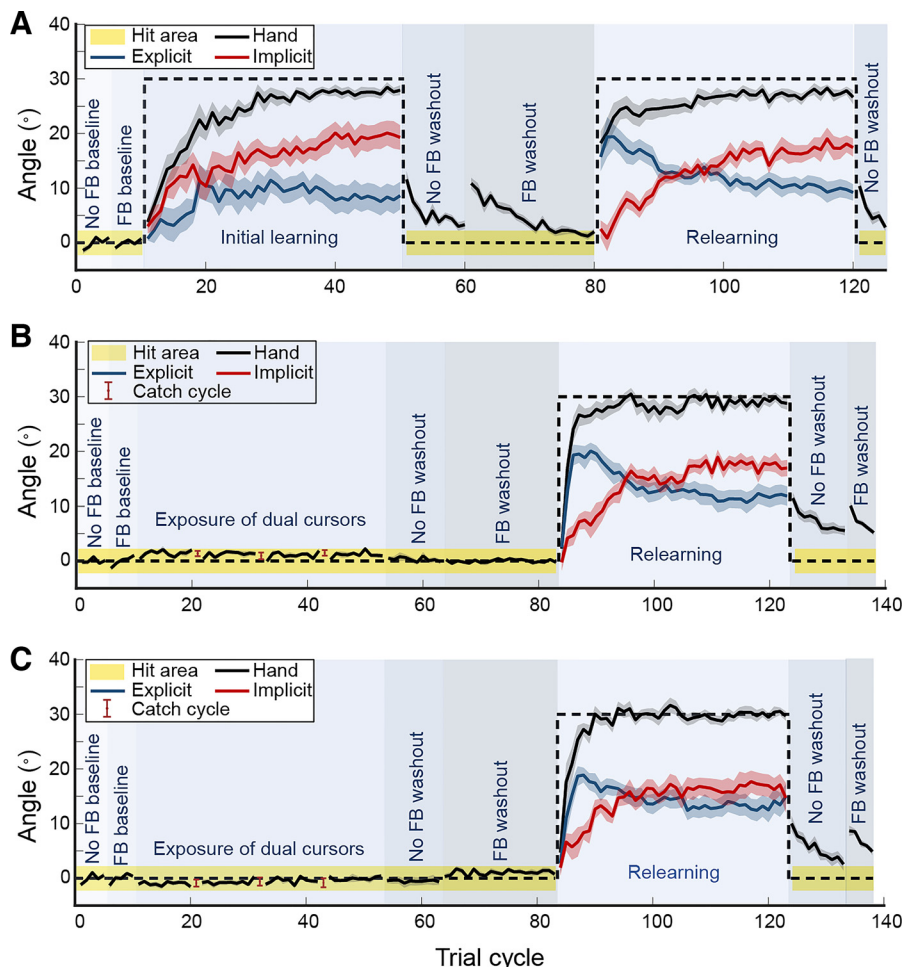


Figure 2. The learning performance in experiment 1. Participants in the Control condition (A) experienced abrupt VMR twice with an interleaved washout period. The savings are apparent in the relearning phase within the initial learning window (shown as a box). Participants in the DCFixed condition were exposed to the second task-irrelevant cursor moving CCW (B) or CW (C) during initial learning, but their hand consistently hit the target. Their hand also showed minimal deviations from the target in catch cycles and during the washout phase, but they showed explicit learning-driven savings in the relearning phase when an abrupt VMR was applied. CCW, counter-clockwise; CW, clockwise; DC, dual cursor; FB, feedback; VMR, visuomotor rotation.

and the initial phase (averaged over the whole initial learning phase) by using paired t tests.

The group differences for other measures were examined by independent one-way ANOVA, followed by post hoc pairwise comparisons with Bonferroni corrections. We set the significance level at $\alpha = 0.05$.

RESULTS

Experiment 1: Task-Irrelevant Feedback Leads to Savings in Subsequent VMR Learning

In *experiment 1*, our Control group learned the abruptly applied VMR perturbations twice with a washout phase in between (Fig. 2A). Their learning patterns resembled previous findings with a significant saving effect during the relearning phase (28, 32). The relearning was significantly faster than the initial learning ($17.02 \pm 1.97^\circ$ vs. $23.84 \pm 1.75^\circ$, respectively; paired t test, $t_{11} = 3.83$, $P = 0.003$). Decomposing the learning into the explicit and implicit components revealed that the saving effect was mostly caused by faster explicit learning. The explicit learning rate amounted to $6.18 \pm 2.16^\circ$ and $16.23 \pm 1.78^\circ$ for the initial learning and the relearning phases, respectively (paired t test, $t_{11} = 5.31$, $P < 0.001$). In fact, the implicit learning rate during the same time window was slightly less in the relearning phase ($10.85 \pm 1.63^\circ$ vs. $7.61 \pm 0.97^\circ$, paired t test, $t_{11} = -2.13$, $P = 0.057$). Clearly, people developed strategic solutions and reused them when they encountered the abrupt visuomotor rotation for the second time. The recall of strategic learning was also evident in the first relearning cycle with a hand deviation of $18.25 \pm 2.11^\circ$ and explicit learning of $15.73 \pm 2.60^\circ$.

The participants in the DC_{Fixed} condition successfully ignored the second cursor and reached the target no matter the second cursor was CW or CCW rotated (Fig. 2, B and C). We defined a successful hit as the hand cursor touched the target, i.e., the distance between the hand cursor and the target was less than 3.9 mm, the sum of the radii of the target and the hand cursor. Throughout the exposure phase, their hand cursor hit the target accurately with an average error of $1.22 \pm 0.30^\circ$ and $-0.55 \pm 0.27^\circ$ for the CCW and CW subgroups, respectively. Although the interspersed no-feedback catch trials produced hand deviations significantly different from zero for the CCW subgroup participants ($t_{11} = 2.67$, $P = 0.021$), the deviations were small with an average error of $1.26 \pm 0.47^\circ$, indicating the hand on average still hit the target. The catch trials of the CW subgroup did not produce significant hand deviation from zero with an average error of $-0.78 \pm 0.62^\circ$ ($t_{11} = -1.25$, $P = 0.236$). Furthermore, in the subsequent washout phase without any visual feedback, the participants showed minimal aftereffect when they were reminded to aim directly to the target (for the first washout cycle, CCW subgroup: $0.52 \pm 0.31^\circ$, $t_{11} = 1.66$, $P = 0.125$; CW subgroup: $-0.43 \pm 0.47^\circ$, $t_{11} = -0.915$, $P = 0.380$). These results thus suggested a lack of implicit adaptation to the rotated second cursor.

We also examined changes in RT and MT when the second cursor was introduced in the initial learning phase. For the CCW subgroup, either RT or MT differed between the baseline phase and the initial learning phase (RT: 0.46 ± 0.03 s vs. 0.48 ± 0.05 s, paired t test, $t_{11} = -1.168$, $P = 0.267$; MT: 0.27 ± 0.02 s vs. 0.25 ± 0.01 s, $t_{11} = 2.049$, $P = 0.065$). For the

CW subgroup, both RT or MT showed a significant decrease from the baseline phase to the initial learning phase (RT: 0.50 ± 0.03 s vs. 0.44 ± 0.02 s, paired t test, $t_{11} = 5.00$, $P < 0.001$; MT: 0.28 ± 0.01 s vs. 0.23 ± 0.01 s, $t_{11} = 3.432$, $P < 0.01$). The decrease possibly reflects a learning effect. Overall, a lack of increase in RT and MT speaks against the hypothesis that our participants covertly simulated the reaiming strategy for countering the task-irrelevant cursor.

Importantly, when subsequently learning the abrupt VMR perturbations, both CCW and CW subgroups exhibited a saving effect: their learning rate was $26.40 \pm 1.02^\circ$ and $26.87 \pm 0.97^\circ$, respectively, significantly faster than the Control group's initial learning (Fig. 3A, left). One-way ANOVA yielded a significant main effect of group ($F_{2,33} = 15.7$, $P < 0.001$), whereas post hoc comparisons found that two subgroups learned similarly fast ($26.40 \pm 1.02^\circ$ vs. $26.87 \pm 0.97^\circ$, $P = 1.000$) but both learned faster than the Control group's first learning ($P < 0.001$ for both post hoc comparisons). In fact, their learning rate was comparable to the Control group's second learning ($F_{2,33} = 1.58$, $P = 0.222$). Their savings were predominantly caused by better explicit learning as one-way ANOVA on the explicit learning rate revealed significant group difference (compared with the Control group's initial learning, $F_{2,33} = 14.465$, $P < 0.001$). The explicit learning rate amounted to $17.50 \pm 1.35^\circ$ and $16.38 \pm 1.26^\circ$ for the CCW and CW subgroups, respectively (Fig. 3A, middle). In contrast, their implicit learning did not differ from that of the Control group (CCW subgroup: $8.91 \pm 1.14^\circ$, CW subgroup: $10.49 \pm 1.19^\circ$, $F_{2,33} = 0.594$, $P = 0.558$; Fig. 3C, right). It is worth noting that the two subgroups did not show any sign of strategic learning in the first cycle of the relearning phase, with small reaiming angles of $2.50 \pm 2.10^\circ$ and $2.76 \pm 1.80^\circ$ for the CCW and CW subgroups, respectively. This lack of reaiming strategy was evident when we compared their reaiming angle to that of the Control group ($F_{2,33} = 11.909$, $P < 0.001$). Thus, after dual-cursor exposure, both subgroups formed strategic solutions for VMR significantly faster than the naïve controls, even though they did not show signs of implicit and explicit learning during exposure.

Experiment 2: Learning of Task-Irrelevant Feedback Is Not Affected by the Randomness of Feedback Size

Experiment 1 found that exposure to task-irrelevant feedback with an angular visuomotor relationship leads to faster strategic learning, irrespective of the direction of the task-irrelevant feedback. However, the visuomotor angle was the same 30° for the exposure and the subsequent VMR adaptation. *Experiment 2* aimed to rule out the possibility that the rote memorization of the 30° oblique angle leads to the saving effect. The participants in the DC_{Random} condition experienced a task-irrelevant cursor with random angle sizes, and even the average angle size differed from the to-be-learned 30° . Half of the participants experienced CCW rotation, and the other half experienced CW rotation during initial learning, but their learning patterns were similar. Thus, we pooled their data and presented their average behaviors (Fig. 3B). First, the participants did not show any immediate influence of the dual cursor during exposure: they hit the target successfully with an average error of $0.73 \pm 0.24^\circ$, a performance similar to that of the DC_{Fixed} participants in the *experiment 1*. The catch cycles also showed minimal hand deviations from the target when no

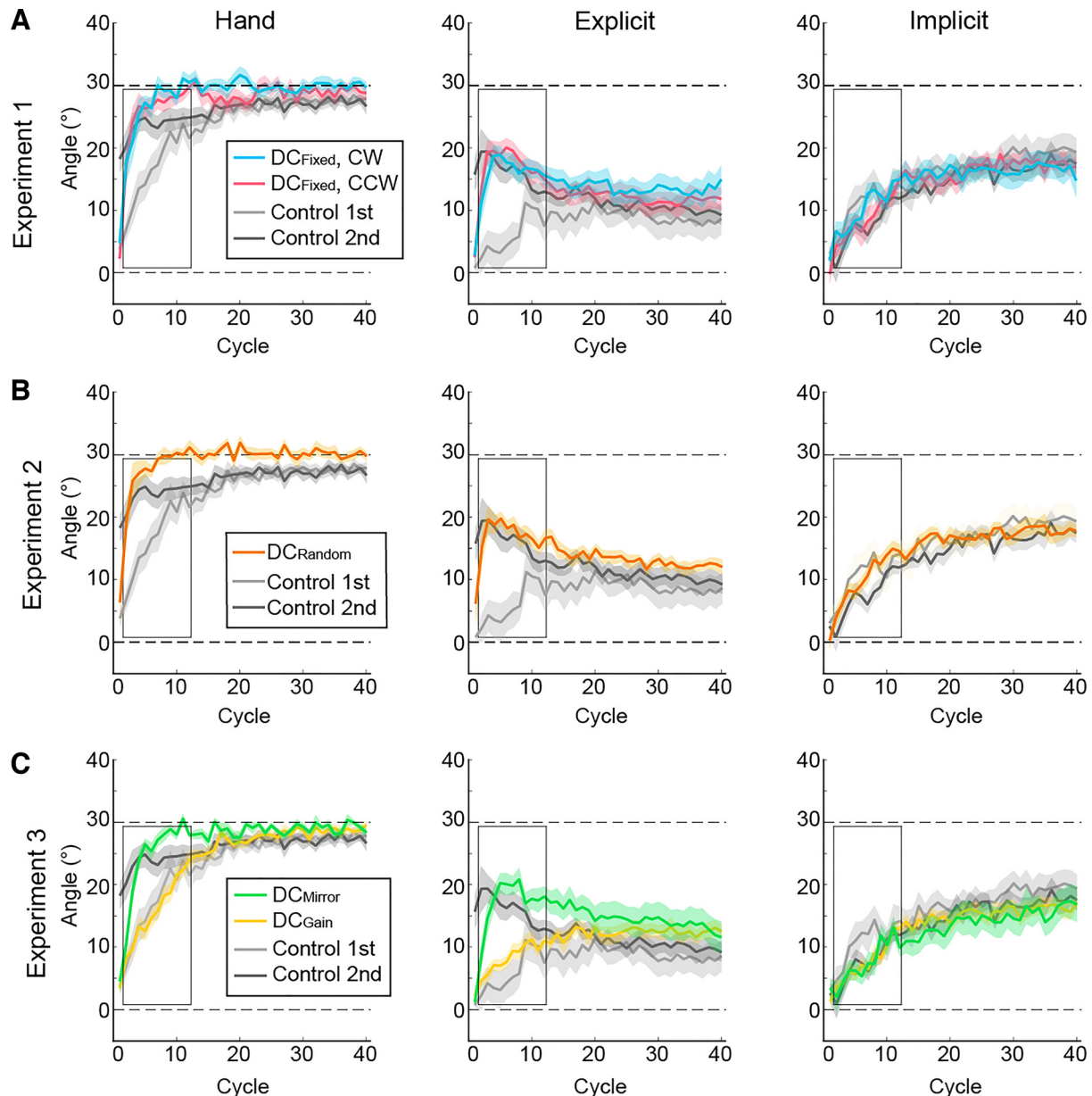


Figure 3. The adaptation to the 30° visuomotor rotation following the exposure of task-irrelevant feedback from all experimental conditions, including experiments 1 (A), 2 (B), and 3 (C). The performance of the Control group is shown in gray as a comparison in all panels. The *left* panels show the hand's directional deviation from the visual target; the *middle* panels and the *right* panels show explicit and implicit learning, respectively. The box denotes the window of trial cycles for computing savings. The shading denotes the standard error across participants. CCW, counterclockwise; CW, clockwise; DC, dual cursor.

cursor feedback was given ($0.13 \pm 0.58^\circ$; t test against zero, $t_{11} = 0.23$, $P = 0.822$), suggesting that there was no covert recalibration of an internal model. Their first cycle in the no-feedback washout phase yielded minimal hand deviations ($0.36 \pm 0.79^\circ$, $t_{11} = 0.455$, $P = 0.658$). Also similar to *experiment 1*, their movements under the influence of the second cursor did not yield an increase in RT and MT (RT: 0.53 ± 0.05 s vs. 0.49 ± 0.03 s, paired t test, $t_{11} = 1.539$, $P = 0.152$; MT: 0.27 ± 0.02 s vs. 0.25 ± 0.01 s, $t_{11} = 1.461$, $P = 0.172$). Thus, when the second cursor randomly changed its angular offset, our participants appeared to ignore it successfully. Importantly, we observed a similar saving effect in the subsequent, abrupt VMR adaptation (Fig. 3B). Their adaptation rate was significantly faster than the Control group's first learning rate ($27.91 \pm 0.85^\circ$,

$t_{14.944} = 5.07$, $P < 0.001$), and comparable to the Control group's second learning rate ($t_{15.915} = 2.09$, $P = 0.053$). This saving effect was driven by a significantly faster explicit learning rate ($17.47 \pm 1.08^\circ$, $t_{16.196} = 2.09$, $P < 0.001$), not by implicit learning rate ($10.44 \pm 0.68^\circ$, $t_{14.761} = 0.23$, $P < 0.821$). Thus, even when the task-irrelevant cursor randomly varied in rotation size, participants still showed the sign of sensorimotor knowledge for later adaptation.

Experiment 3: Embedded Visuomotor Relation Determines the Learning of Task-Irrelevant Feedback

In *experiments 1* and *2*, the task-irrelevant feedback was a rotated cursor, and we did not find any evidence of implicit adaptation during its exposure. Previous studies have found

that implicit adaptation, manifested as hand deviations without participants' awareness, occurs when the task-irrelevant feedback is shown without the hand cursor (27, 33). To further rule out the possibility that a covert implicit adaptation leads to the saving effect, in the DC_{Mirror} condition, we examined the effect of exposing to a mirrored cursor feedback that conveys a similar visuomotor relationship between hand movement and cursor movement but does not lead to adaptation whatsoever (29). We observed no performance difference between the two subgroups who experienced the dual cursor with horizontal or vertical mirroring (Fig. 1B); thus, we reported their pooled data. The mirrored cursor did not lead to any significant hand deviations during the dual-cursor exposure, with an average hand deviation of merely $-0.17 \pm 0.48^\circ$. The participants also exhibited minimal hand deviations during catch cycles ($0.27 \pm 0.65^\circ$, $t_{11} = 0.42$, $P = 0.685$), suggesting that they did not implicitly adapt to the mirrored cursor. Their RT and MT during the initial learning phase did not change from the baseline (RT: 0.51 ± 0.03 s vs. 0.48 ± 0.02 s, paired t test, $t_{11} = 2.10$, $P = 0.06$; MT: 0.28 ± 0.01 s vs. 0.26 ± 0.02 s, $t_{11} = 1.581$, $P = 0.142$). Their first cycle in the no-feedback washout phase showed no sign of implicit adaptation either ($0.35 \pm 0.60^\circ$, $t_{11} = 0.579$, $P = 0.574$). Critically, these participants showed savings when they subsequently adapted to an abrupt VMR perturbation with a learning rate of $25.07 \pm 0.70^\circ$ (Fig. 3B, left). This learning rate was faster than the control group's first learning ($t_{13.704} = 3.847$, $P = 0.002$) and comparable to their second learning (t test, $t_{22} = 0.655$, $P = 0.519$). The saving effect was observed in the two subgroups who experienced either vertical or horizontal mirroring (see Supplemental Fig. S1 in the online supplemental material: <https://doi.org/10.6084/m9.figshare.14811447>). Similar to experiments 1 and 2, the saving effect was largely driven by a significant increase in the explicit learning ($17.51 \pm 1.29^\circ$, $t_{22} = 4.502$, $P < 0.001$), not by a change in implicit learning ($7.56 \pm 1.05^\circ$, $t_{22} = -1.695$, $P = 0.104$). The DC_{Mirror} participants also showed a similar lack of relearning strategy in their first cycle during the relearning phase (Fig. 3B, middle). The hand deviation was merely $1.20 \pm 0.44^\circ$, significantly less than the corresponding performance in the Control group ($t_{11.618} = -5.508$, $P < 0.001$). Thus, with the exposure to a mirrored cursor instead of a rotated cursor the participants still showed the sign of obtaining necessary sensorimotor knowledge when they subsequently adapted to VMR perturbations.

The participants in the DC_{Gain} condition experienced the task-irrelevant cursor feedback without a visuomotor direction relationship but with a visuomotor gain relationship. As the second cursor moved in the same direction, it did not affect the hand movement direction, which was $0.91 \pm 0.22^\circ$ and $0.85 \pm 0.41^\circ$ for the exposure trials and the catch trials, respectively. The hand deviation in the first cycle of the no-feedback washout phase also did not show any sign of implicit adaptation ($0.22 \pm 0.46^\circ$, $t_{11} = 0.479$, $P = 0.641$). We also examined whether the visuomotor gain of the second cursor affected the participant's movement amplitude. As our task required participants to shooting toward the targets without stopping at them, the start-to-end movement distance could not reflect movement amplitude. Instead, we examined the peak velocity of the shooting movement, a proxy of its movement amplitude, over the exposure period. The peak velocity was not modulated by the visuomotor gain: smaller gains (i.e., gain between 0.4 and 0.6) and larger

gains (i.e., gain between 1.2 and 1.4) yielded similar peak velocity (572.72 ± 32.29 mm/s and 560.94 ± 36.09 mm/s, respectively; paired t test, $t_{11} = 1.468$, $P = 0.17$). We also did not observe any significant change in RT and MT from the baseline phase to the initial learning phase (RT: 0.50 ± 0.03 s vs. 0.49 ± 0.02 s, paired t test, $t_{11} = 0.657$, $P = 0.525$; MT: 0.24 ± 0.01 s vs. 0.24 ± 0.02 s, $t_{11} = 1.581$, $P = 0.142$). Thus, the participants successfully suppressed the second cursor's influence, as we did not observe any movement changes associated with the visuomotor gain of the second cursor. Importantly, the participants did not show any saving effect in the subsequent abrupt VMR adaptation (Fig. 3C). Compared with the Control group, these participants did not show any improvement in learning rate ($16.29 \pm 1.15^\circ$; not different from the Control group's initial learning, $t_{17.726} = -0.320$, $P = 0.753$; significantly slower than the Control group's second learning, $t_{22} = -3.602$, $P = 0.002$). In fact, both of their explicit learning rate and implicit learning rate were comparable to those of the Control group's initial learning (explicit: $8.49 \pm 0.89^\circ$, $t_{14.632} = 0.989$, $P = 0.333$; implicit: $7.80 \pm 0.69^\circ$, $t_{14.842} = -1.721$, $P = 0.099$). Thus, the DC_{Gain} group adapted to the abrupt VMR as if they were naïve to this type of perturbation in stark contrast to other conditions with task-irrelevant feedback.

In sum, all experimental groups were exposed to a task-irrelevant second cursor and showed no sign of adapted behavior during exposure. The participants in the DC_{Fixed} and DC_{Random} conditions experienced rotated cursor feedback, which varied in the signs or magnitudes of rotation angles; the participants in the DC_{Mirror} condition experienced a mirrored cursor feedback, which has been shown related to skill acquisition; the participants in the DC_{Gain} condition experienced a gain-scaled cursor without directional manipulation. Compared with the Control group's first learning, all but the DC_{Gain} condition showed savings in the subsequent VMR adaptation ($F_{5,66} = 13.726$, $P < 0.001$; post hoc pairwise comparisons shown in Fig. 4). The occurrence and the lack of savings in these groups were also evidenced by comparing their relearning performance to the relearning of the Control group ($F_{5,66} = 7.342$, $P < 0.001$; only the DC_{Gain} condition showed significantly slower learning than other conditions). We performed the same ANOVAs for the explicit and implicit learning rates separately (Fig. 4). We confirmed that the saving effect was driven by faster explicit learning (compared with the Control group's first learning: $F_{5,66} = 13.726$, $P < 0.001$; compared to the Control group's relearning: $F_{5,66} = 19.250$, $P < 0.001$). Shown by post hoc comparisons, all experimental conditions except the DC_{Gain} condition have a significantly larger explicit learning rate than the first learning of the Control group; similarly, only the DC_{Gain} condition showed a significantly smaller explicit learning rate than the relearning of the Control group. Implicit learning rate remained unchanged in all experimental conditions (compared with the Control group's first learning: $F_{5,66} = 1.699$, $P = 0.147$; compared with the Control group's relearning: $F_{5,66} = 1.996$, $P = 0.091$).

DISCUSSION

We find that people show expedited learning of visuomotor rotation after exposure to task-irrelevant feedback. This saving

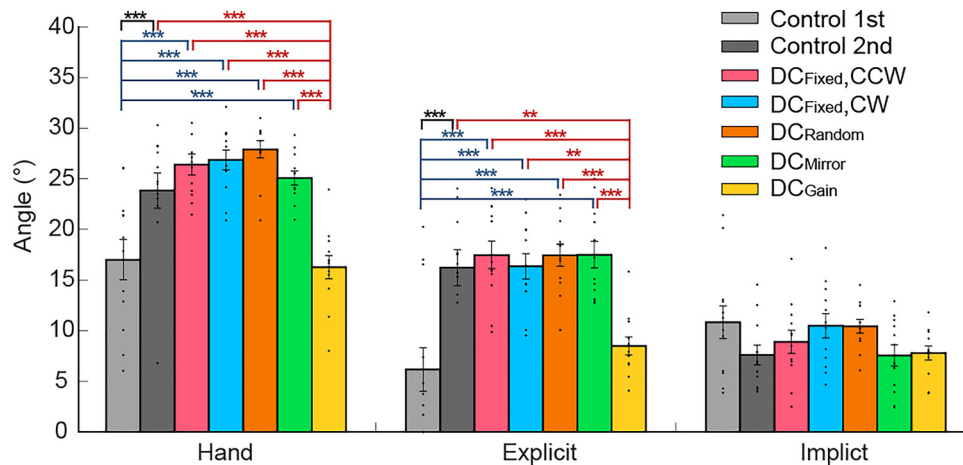


Figure 4. A summary of findings from the three experiments. The relearning rates of the experimental groups are shown with the learning and relearning rates of the Control condition. Total learning rate, explicit learning rate, and implicit learning rate were shown separately. Two separate ANOVAs were performed, one for comparing all experimental conditions with the first learning of the Control group, the other for comparing with the relearning of the Control group. The post hoc pairwise comparisons are shown separately for these two ANOVAs (depicted by blue and red, respectively). Note, only the DC_{Gain} condition did not show faster total learning and explicit learning than the Control group's first learning. Implicit learning remained unchanged between conditions. $**P < 0.01$ and $***P < 0.001$. CCW, counterclockwise; CW, clockwise; DC, dual cursor.

effect is evident as long as the task-irrelevant feedback is angularly offset from the intended action, independent from the feedback's direction (*experiment 1*), angular size (*experiment 2*), or its embedding task (*experiment 3*). In contrast, when the task-irrelevant feedback carries a different, gain-scaled relationship with the intended action without angular offset, it no longer leads to faster learning in the subsequent visuomotor rotation adaptation (*experiment 3*). Since the exposure phase does not involve implicit or arguably, strategic learning to visual perturbations, our findings support that abstract sensorimotor knowledge is acquired from the task-irrelevant feedback and leads to faster strategic learning and savings.

In contrast to the conventional visuomotor rotation paradigm, the rotated second cursor serves as the task-irrelevant feedback without perturbing the main movement. The hand cursor was a veridical representation of the hand, reaching accurately to the target during the dual-cursor exposure with minimal target error (e.g., Fig. 2, B and C). Furthermore, the task-irrelevant feedback appeared not to produce sensory prediction error (SPE), as we observed no aftereffect in catch trials. The catch trial is an effective means to probe SPE-based implicit learning for task-relevant feedback (34) and task-irrelevant feedback (35). Neither did we observe any sign of aftereffect at the beginning of the no-feedback wash-out phase. Thus, our results are distinct from the findings in the so-called error-clamp learning paradigm, which only displays a clamped, directionally deviant cursor without the hand cursor (27). Although the clamped cursor is also regarded as irrelevant feedback, the researchers found that participants gradually deviate their hands from the straight movement path toward the target. This obligatory learning is viewed as implicit, SPE-based learning where the irrelevant feedback is possibly interpreted (mistakenly) as the visual representation of the moving hand (27, 33). Our dual cursor paradigm effectively prevented this implicit learning process by asking participants to aim their hand cursor to the target. Thus, the hand cursor helped the participants to discount the influence of the clamped cursor, which was then less

likely to be mistakenly viewed as a hand representation. In sum, our dual-cursor paradigm does not provide salient target error or sensory prediction error since the exposure phase does not invoke strategic learning or implicit learning. Furthermore, we did not find any movement changes that were associated with acquiring the reaiming strategy during the exposure. Typically, forming or recalling the reaiming strategy increases reaction time (36, 37). However, we did not observe an increase in reaction time or movement time during the dual-cursor exposure for all the experimental conditions. We also regard unlikely a covert simulation of the reaiming strategy as the second cursor's angular offset changed randomly in magnitude (as in *experiment 2*) and in both magnitude and direction signs (as in the DC_{Mirror} group of *experiment 3*), which make mental rehearsal of the reaiming strategy difficult. Then, how is the ensuing savings possible if either of the two error-based learning is present?

The learning component that leads to savings in the visuomotor rotation has been attributed to the memory of errors (38) or the recall of acquired cognitive strategy (39), neither of which readily explains our findings. The error-sensitivity account asserts that savings are caused by increased sensitivity to motor errors that have been exposed to and thus memorized (38). Thus, the current model of this account would require exposure to similar motor errors during learning and relearning (40–42). However, our participants did not show any sign of SPE-driven adaptation during exposure to the task-irrelevant feedback, neither did they experience any obvious target error. It can be argued that the second cursor would produce covert sensory prediction error, similar to the single-cursor error-clamp learning (27), and the influence of this sensory prediction error did not manifest itself during the exposure. However, even this covert learning idea cannot explain why the second cursor with the opposite directional deviation (the CCW subgroup in the DC_{Fixed} condition of *experiment 1*) and random rotation size (the DC_{Random} condition in *experiment 2*) yielded the same saving effect, although the participants did not experience similar errors.

Alternatively, the strategic learning account of savings posits that expedited relearning results from a recall of previously acquired strategic solutions to counter perturbations (39). The strategic learning account receives extensive supports, especially for adaptation to an abruptly applied VMR perturbation (36, 39, 43). Explicit aiming reports showed that people developed reaiming strategy gradually and recalled this strategy during relearning (43), a finding replicated by our Control group in *experiment 1*. People also found that a few trials of perturbation trials with large rotations can lead to savings, which is unlikely if savings are driven by the slow and gradual SPE-based adaptation (39). Anyhow, this account necessitates the formation of a strategic solution during initial learning. However, our participants aimed straight ahead to the target without any reaiming strategy when exposed to the task-irrelevant feedback. This lack of strategy acquisition also manifested itself as near-zero explicit learning in the first cycle of the relearning phase. This is in sharp contrast to the Control group's relearning behavior since their explicit learning reached a high level ($15.73 \pm 2.60^\circ$ for a 30° VMR, Fig. 2A) in the first relearning cycle. Across all our test groups, the savings are shown as a quick formation of strategy in the subsequent relearning cycles, not a quick recall of strategic learning.

We thus postulate that the knowledge about sensorimotor contingency in the adaptation task underlies the observed saving effect. When exposed to task-irrelevant feedback, people observe a consistent visuomotor relationship between the hand movement and the second cursor movement and acquire this sensorimotor contingency without any behavioral expression. When the motor system subsequently encounters a VMR perturbation, the sensorimotor knowledge can facilitate strategic learning since the motor system recognizes a similar visuomotor contingency in the VMR perturbation. This sensorimotor knowledge is elusive from typical measures of strategic learning, i.e., verbal reports (6) or even exclusion (45, 46). Our results thus suggest that the dichotomy of explicit versus implicit learning in motor adaptation be a result of available measurement paradigms, and the actual processes underlying the adaptation are more multifaceted (47).

Sensorimotor knowledge can also explain a puzzling finding with the conventional error-clamp perturbation (28). After implicitly adapting to the error clamp, people exhibited faster adaptation to an abrupt-induced VMR than naïve control. This appears to suggest that implicit learning could lead to better strategic learning. However, close inspection of these participants' behaviors revealed a similar relearning pattern, as in the current study: the explicit learning was initially small in the first relearning cycle, and the saving effect was largely driven by a faster formation of explicit strategy in later cycles. Thus, we postulate that the observed savings after the error-clamp adaptation is also enabled by acquired motor knowledge (28). In fact, error-clamp learning, though widely accepted as implicit adaptation (27, 33), inevitably leads to the acquisition of sensorimotor knowledge. After all, the participants in this paradigm are informed to ignore the clamped cursor before the experiment, and the instruction makes it explicit to the participants the special visuomotor contingency they would encounter. Thus, the error-clamp paradigm inevitably involves informed sensorimotor know-

ledge, whose effect is latent during clamp learning but may contribute to the subsequent adaptation to a similar VMR perturbation (28). This subtle knowledge shall be taken into consideration when we interpret the behavioral results of error-clamp learning.

Learning of sensorimotor knowledge from irrelevant feedback is akin to structure learning, which refers to the process of discovering the causal structures between different observable variables in cognitive science (48). In the motor domain, structure learning is about discovering the intrinsic structure of sensorimotor tasks (49). After acquiring a task structure, the subsequent motor learning can be facilitated if the to-be-learned task shares the same structure, possibly because that the subsequent learning can be simplified as setting a new set of control parameters for the learned structure (50). Thus, structure learning is regarded as the extraction of invariants between different input-output mappings, which can be later used for reducing the dimensionality of the search space during motor learning (50). The structure of the task is conceptually similar to the sensorimotor knowledge we posit here. However, previous studies on structure learning still demand participants to practice the motor task physically (49, 51). One extreme case of fast acquisition of task structure of visuomotor rotation is that people can acquire the aiming strategy when exposed to abrupt VMR perturbation for a few trials (39). Instead, our study demonstrates that sensorimotor knowledge can be learned via exposure to task-irrelevant feedback without motor practice. Whether this type of learning can be generalized to more complex motor adaptation tasks other than simple visuomotor rotation warrants further investigations.

The role of sensorimotor knowledge in motor learning has been studied for both skill learning and motor adaptation. For skill learning, performance improvements are attributed to enhanced motor acuity and the acquisition of propositional knowledge (4, 5). For motor adaptation, the performance improvements are attributed to implicit learning and acquisition of explicit strategy (6). Previous research on sensorimotor knowledge emphasizes its propositional, declarative, or verbalizable nature. For skill learning, explicit verbal instruction has been shown to benefit learning by its motivational value (52) or by better attention allocation (53). For motor adaptation, the explicit strategy can directly affect adaptation performance (21, 54) and is often assessed by verbal reports (6) or verbal instruction to withdraw from using the strategy (45, 46). Instead of acquiring strategy by verbal instruction, our findings indicate that sensorimotor knowledge can be acquired by sensorimotor experience without a learning task. Indeed, in the broad domain of cognitive sciences, there are two highly interactive ways of acquiring conceptual knowledge, i.e., by verbal experience and by sensorimotor experience (55–57). The specific conceptual knowledge in our task is about the directional relationship between action and its visual representations, which was acquired by sensorimotor experience with the task-irrelevant feedback.

Previous studies have found that daily sensorimotor experience benefits motor adaptation, possibly via the acquired sensorimotor knowledge. For example, one of our previous studies found that people who had never used computers generalized poorly after adapting to novel visuomotor gain

perturbations, whereas a 2-wk training of computer mouse use enabled them to perform as well as computer users (58). Visuomotor gain adaptation requires people to adapt to a novel movement amplitude ratio between the hand and the cursor. In fact, different visuomotor gains are inherent in controlling different computer mice, leading to a common but unnoticed sensorimotor knowledge among us. The effect of this sensorimotor knowledge on motor adaptation would be left unchecked until those naïve computer users were tested with the classical motor adaptation paradigm (58). In another study, we have found that adaptation to weight changes of the hand generalizes broader than the force field adaptation, despite both perturbations mechanically disturbing hand movements (59). We postulate that hand weight changes are common in daily life (e.g., the weight of a handheld object changes frequently), but force field perturbations from a robotic manipulandum are rare and limited to laboratory settings. Similar to the finding of computer use, more sensorimotor experience of the weight changes is possibly associated with better sensorimotor knowledge of this type of perturbations and thus leads to a broader generalization of its motor adaptation.

Our findings demonstrate that the benefits of task-irrelevant feedback differ between motor learning and perceptual learning. First, perceptual learning of irrelevant feedback only happens when people do not attend to and unaware of the irrelevant feedback. The task-irrelevant features can be learned only when they are below or near the detection threshold; if they are above the detection threshold, the learning is also prevented (9, 11). In contrast, in our dual-cursor experiment, the participants intentionally suppressed the influence of the second cursor by focusing on the main cursor; otherwise, their hand would have deviated from the straight line reaching and exhibited implicit learning behaviors as in the typical error-clamp learning paradigm (27). Thus, distinct from findings in perceptual learning, the task-irrelevant feedback is well perceived and its influence is actively suppressed in our paradigm. Second, perceptual learning of the task-irrelevant feedback occurs on the lower level of the visual hierarchy (11). Our motor counterpart is related to the acquisition of sensorimotor knowledge from the visuomotor experience. The expedited formation of explicit strategy during relearning and its independence from feedback variations (direction and size) suggest that the task-irrelevant feedback leads to high-level representations of sensorimotor contingency. Despite the difference, both motor and perceptual learning of task-irrelevant feedback can be viewed as unsupervised learning without a task (60, 61).

Our findings of the learning from task-irrelevant feedback also differ from typical observational learning in the motor domain. Observational learning is common in sports skill acquisition in the form of coaches' demonstration. Directly related to the current study is the beneficial effect of observing expert's movements in motor adaptation paradigms. People have found that observing the movements of someone adapting to a force field can lead to better learning afterward (16). This benefit is independent of the conscious awareness of the observer, as distraction by a simultaneous working memory task does not prevent observational learning. Researchers suggested that the observer forms a neural representation of the environment's novel mechanical

properties for motor adaptation (16, 62), instead of learning what movements to make for skill acquisition (63, 64). However, though also manifested by facilitated motor adaptation, our learning of task-irrelevant feedback differs from observational learning. First, observational learning is abolished when the hand performs an irrelevant movement during observation, while our main task of reaching the target does not prevent the learning. Second, observation of adapting to an opposite force field perturbation leads to reduced learning as opposed to facilitated learning afterward (16), whereas our *experiments 1* and *2* showed similar learning when participants are exposed to an opposite feedback error. Thus, we conclude that task-irrelevant feedback learning is distinct from previously documented observational learning in motor adaptation. It involves acquiring sensorimotor knowledge of visuomotor contingency conveyed by the feedback.

In conclusion, the present study finds that observing task-irrelevant feedback during movement can expedite later motor adaptation. This saving effect does not result from implicit adaptation or a recall of motor strategy. Rather, given its independence of variations in feedback feature and task type, the specific learning probably involves the acquisition of the sensorimotor knowledge of the to-be-learned visuomotor relationship. In motor learning, the learning of the task-irrelevant feedback is distinct from observational learning for its abstract nature and from structure learning for its lack of motor practice. Our findings highlight the need to incorporate conceptual sensorimotor knowledge for the seemingly simple motor adaptation.

SUPPLEMENTAL DATA

Supplemental Fig. S1: <https://doi.org/10.6084/m9.figshare.14811447>.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

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

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