

Interference from mere thinking: mental rehearsal temporarily disrupts recall of motor memory

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Yin C, Wei K. Interference from mere thinking: mental rehearsal temporarily disrupts recall of motor memory. *J Neurophysiol* 112: 594–602, 2014. First published May 7, 2014; doi:10.1152/jn.00070.2014.—Interference between successively learned tasks is widely investigated to study motor memory. However, how simultaneously learned motor memories interact with each other has been rarely studied despite its prevalence in daily life. Assuming that motor memory shares common neural mechanisms with declarative memory system, we made intuitive predictions that mental rehearsal, as opposed to further practice, of one motor memory will temporarily impair the recall of another simultaneously learned memory. Subjects simultaneously learned two sensorimotor tasks, i.e., visuomotor rotation and gain. They retrieved one memory by either practice or mental rehearsal and then had their memory evaluated. We found that mental rehearsal, instead of execution, impaired the recall of unretrieved memory. This impairment was content-independent, i.e., retrieving either gain or rotation impaired the other memory. Hence, conscious recollection of one motor memory interferes with the recall of another memory. This is analogous to retrieval-induced forgetting in declarative memory, suggesting a common neural process across memory systems. Our findings indicate that motor imagery is sufficient to induce interference between motor memories. Mental rehearsal, currently widely regarded as beneficial for motor performance, negatively affects memory recall when it is exercised for a subset of memorized items.

motor memory; mental rehearsal; motor imagery; retrieval-induced forgetting; sensorimotor learning; motor learning

THE FORMATION OF MOTOR MEMORY involves two distinct stages. In the first stage, newly learned skills are stored in short-term working memory, and they are prone to interference from subsequent motor learning (Tong and Flanagan 2003). In the second stage, learning is consolidated into long-term memory (Brashers-Krug et al. 1996; Muellbacher et al. 2002; Shadmehr and Brashers-Krug 1997). Consolidation is often evaluated by the degree of resistance to retrograde interference (Krakauer et al. 2005), i.e., interference by the second task on the learning of the first task. So far, this interference effect has been extensively investigated in motor adaptation using the paradigm *task A* → *task B* → *task A*. Oftentimes, *tasks A* and *B* involve the same type of perturbation but with opposite perturbing effects, e.g., clockwise and counterclockwise visuomotor rotations (Krakauer et al. 2005) or force fields (Brashers-Krug et al. 1996). A typical finding is that *memory A* is not consolidated if *tasks A* and *B* are practiced in close succession, suggesting opposite learnings compete for common working memory resources (Tong et al. 2002). In contrast, the consolidation of *memory A* is not affected by *task B* if two successive

learnings involve different types of perturbations (Krakauer et al. 1999) or even different motor tasks (Tong and Flanagan 2003). Although the area has focused on interaction between two successively learned tasks, people in reality learn different motor tasks simultaneously, like a typical basketball training session probably consists of practices of dribble, jump shot, foul shot, and pick and roll. Whether and how simultaneously learned motor memories interfere with each other have not been systematically investigated.

On the other hand, interference effects of simultaneous learned information have long been studied in the realm of declarative memory. A robust finding is that retrieving a particular memory impairs the recall of a related memory, a phenomenon called retrieval-induced forgetting (RIF; Anderson et al. 1994). RIF effect typically arises when subjects actively retrieve memorized items with conscious recollection but not when they further strengthen these items through relearning or reexposure (Anderson et al. 2000; Bäuml and Aslan 2004; Hanslmayr et al. 2010). If this effect between multiple memories extends to motor memory, it will lead us to two unintuitive predictions: for two simultaneously learned motor memories, active thinking (conscious retrieval) of one motor memory will impair subsequent recall of the other motor memory. In contrast, further executing (practice) of one task will not impair immediate recall of the other motor memory. In other words, interference between motor memories can be elicited by mental rehearsal without motor execution, which is typically used in motor learning studies. These are rather strong predictions since impairment of motor memory by mental rehearsal has never been documented. On the contrary, mental rehearsal is widely regarded as beneficial for maintaining motor memory (Malouin et al. 2013).

To test these predictions, we asked subjects to learn concurrently two sensorimotor mappings during hand reaching. The first one was visuomotor rotation where the visual representation of the moving hand was rotated while reaching toward a left target (Cunningham 1989; Roby-Brami and Burnod 1995). The second was a novel visuomotor gain where the movement extent of the visual presentation was amplified while reaching toward a right target (Bock 1992; Vindras and Viviani 2002). We expected that subjects could learn two visuomotor transformations simultaneously with interleaved training trials as previous studies have evidenced that separate neural substrates underlie the learning of these two transformations (Turner et al. 2003). After both transformations were acquired, subjects retrieved one of the motor memories by motor execution (*experiment 1*), mental rehearsal facilitated by visual cues (*experiment 2*), or mental rehearsal with passive movements realized by robotic force (*experiment 3*). After retrieval, both memories

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were evaluated and compared with their respective baselines obtained in Control Groups who remained idle for the same period of time as retrieval.

MATERIALS AND METHODS

Subjects. One hundred twelve right-handed subjects participated in the study. In *experiments 1–3*, all subjects learned both visuomotor mappings, and these experiments had a total of eight groups of subjects ($n = 12$ each). The average age in years of the participants for the eight groups was 22.3 ± 4.8 (SD, same below), 22.3 ± 3.1 , 22.0 ± 2.6 , 21.3 ± 1.7 , 21.2 ± 3.3 , 21.9 ± 2.6 , 23.4 ± 3.7 , and 22.9 ± 4.3 . The number of men was 6, 4, 5, 6, 3, 7, 5, and 7, respectively. In two control experiments, two different sets of subjects ($n = 8$) were recruited to learn a single type of visuomotor mapping, either visuomotor rotation or gain. The average age in years of these participants was 21.8 ± 4.0 and 23.4 ± 5.3 , respectively. The number of men was 3 and 2, respectively. All subjects were naïve to the purpose of the experiments, signed an institutionally approved consent form, and were paid to participate. All experimental procedures were approved by the institutional review board of Peking University.

General experimental procedure. Subjects sat behind a desk and moved their right, dominant hand on the desktop. Their vision of the hand and arm was blocked by a semisilvered mirror placed horizontally at chest level. The movement of the index finger tip was measured at a frequency of 200 Hz with a resolution of 0.05 mm (Codamotion, Charnwood Dynamics). Visual feedback was projected top-down from an LCD projector (display frequency 75 Hz; P1270, Acer) mounted 1.45 m above a horizontally placed back-projection screen. The image was then reflected in the mirror, which subjects looked into (Fig. 1).

Subjects were instructed to make straight and uncorrected reaching movements to either of the two horizontally displayed targets in successive attempts (Fig. 1). Two targets were 100 mm from the starting position and were both displayed as white discs, 4 pixels in diameter. Subjects experienced two distinct visuomotor mappings associated with these two targets: while moving toward the left target, subjects experienced visuomotor rotation perturbations where visual representation of the hand was rotated 30° counterclockwise; while moving toward the right target, they experienced a visuomotor gain perturbation where the gain between the actual hand and its endpoint display was set at 0.6 (instead of a veridical value of 1). Subjects should move toward 30° upper left to compensate for the imposed rotation; they should move 60 mm horizontally to the right to reach the 100-mm distance target to compensate for the imposed gain. For visuomotor rotation trials, the distance feedback was always veridical. For visuomotor gain trials, the directional feedback was always veridical.

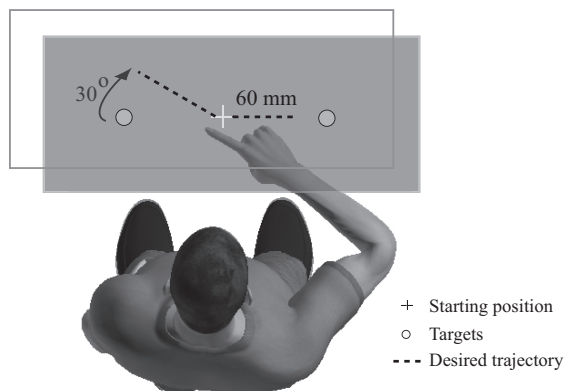


Fig. 1. Illustration of experimental setup and reach targets on the screen. The cursor representation of the hand is associated with visuomotor rotation and visuomotor gain when moving to the left and right target, respectively.

At the beginning of each trial, subjects rested their right index finger on a 4-mm thin plastic disc glued on the desktop. The disc was used to facilitate subjects to position their finger on the starting position. A visual starting position, depicted as a yellow cross (4 pixels each line), was overlaid on the plastic disc. A cursor (green disc, 4 pixels in diameter) representing the finger position was only visible within 8 mm around the starting position. Once the finger stayed at the starting point for 100 ms, one of the two targets would appear, and a beep sound was played by a computer speaker to signal subjects to move. A beep sound was also played once subjects stopped the reach to signal them to bring the finger back to the starting position for the next trial. To make sure that people can learn the two tasks effectively, we adopted commonly used feedback structure during active reaching: visuomotor rotation was imposed with continuous cursor feedback (Krakauer et al. 2005; Tong and Flanagan 2003), whereas visuomotor gain was imposed with terminal feedback when the cursor was only briefly displayed for 100 ms after the hand stopped (Pearson et al. 2010; Wei et al. 2014). A recent study has suggested that these two feedback structures produced similar course of adaptation for visuomotor rotation (Taylor et al. 2013). A low-pitched tone warned the subject if he or she moved too slow (movement time >550 ms). Before formal data collection, they familiarized themselves with the required movement speed.

Experiment 1. This experiment aimed to examine whether active execution of one task could interfere with the short-term memory of another task after both visuomotor transformations were learned. The experiment involved four phases. In the familiarization phase, subjects moved to each target 10 times in a random sequence without any perturbations. During the subsequent training phase, subjects moved to each target 75 times in a random sequence with aforementioned perturbations imposed. There were also 10 randomly interspersed catch trials (5 for each target) when no cursor feedback was given. These trials were presented after the 30th training trial when the learning was assumed to reach a plateau. In the retrieval phase, subjects in Control Group were instructed to sit idle and perform a backward-counting task. Other subjects either made reaches to the left (Rotation-Retrieval Group) or to the right (Gain-Retrieval Group) target for 20 trials with their corresponding perturbations. The retrieval phase lasted for 1 min for all groups. Finally, in the 4th retest phase, subjects moved to both targets 5 times in a random sequence without visual feedback. Their memory about 2 perturbations was thus assessed.

Experiment 2. This experiment aimed to examine whether mental rehearsal of one task can interfere with the recall of another memory. It shared the same Control Group with *experiment 1*. The procedure was identical to that of *experiment 1* except for the retrieval phase. Instead of executing the task, subjects either actively imagined to reach to the left (Rotation-Retrieval Group) or to the right target (Gain-Retrieval Group) for 20 trials. To facilitate trial-by-trial imagery, we provided the sequence of visual cues that subjects normally perceived during their training trials: the starting position was extinguished and the target was lit up to signal the reach onset, the target was extinguished to signal the end of the reach, and the starting position was lit up again to signal the repositioning of hand to the starting position. The sequence of these cues were timed according to the average timing from the last 20 training trials. To make sure that they can generate somatosensory images of the movements, the experimenter asked the subjects whether they could sense their arms moving (Deiber et al. 1998; Lacourse et al. 2005), and all subjects answered positively. The finger cursor was not moved but only shown briefly at the starting position for 1 s. This retrieval phase similarly lasted for 1 min.

Experiment 3. Our aim here was to examine whether mental rehearsal facilitated by passive movements, implemented by a robot, can interfere with the recall of unretrieved memory. The procedure was identical to that of *experiment 1* except for the retrieval phase. Since the retrieval phase was slightly longer than in *experiment 1* (90

s compared with 60 s due to robot use), we recruited a separate Control Group who sat idle through the retrieval phase. For test groups, subjects grabbed a stylus end of a robotic arm (PHANTOM Desktop, SensAble) and placed its tip at the starting position. They were instructed to relax and not to interfere with the movement of the robot. Their hand was then passively pulled by the robot to the left (Rotation-Retrieval Group) or right (Gain-Retrieval Group) target. Similar visual feedback was given as in *experiment 2*. Once the passive reach was finished, subjects took the robotic arm back to the starting position. The target trajectory the robot was programmed to achieve is similar, in terms of displacement and duration, to the average trajectory that subjects performed at the end of the training phase. This retrieval phase had 20 trials.

Data analysis. The direction error (DirErr) and the extent error (ExtErr) of hand reaches were used to quantify the performance in visuomotor and gain learning, respectively. The DirErr was taken as the angular difference between the desired direction (30° clockwise of the target direction) and the actual movement direction (the direction of the vector defined between the starting position and the reaching endpoint). The ExtErr was calculated as the difference between the desired extent (60 mm) and the achieved extent. These two error measures were then converted to the percentage of learning. For visuomotor rotation, it is:

$$100 \times \left(1 - \frac{\text{DirErr}}{30^\circ} \right).$$

For visuomotor gain, it is:

$$100 \times \left[1 - \frac{\text{ExtErr}}{100 \times (1 - 0.6)} \right].$$

The learning achieved after training and before retrieval was quantified either by catch trials randomly interspersed during the late learning phase or by the last five training trials. The average performance in the retest phase served as an indicator of retained learning after the retrieval phase. The memory decay was quantified as the

performance difference between the end of training (pretest) and the retest.

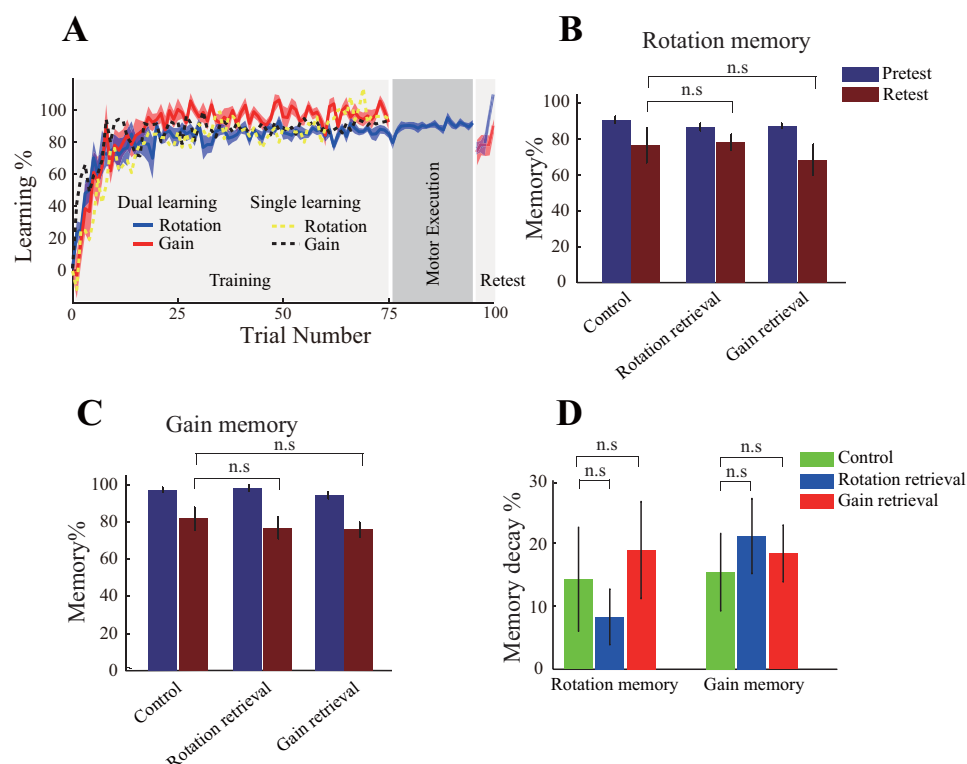
We are mostly interested in whether retrieval can induce interference when comparing with the baseline conditions without retrieval. Thus we compared each test group with its Control Group using two-sample *t*-tests. One-way ANOVA was used when multiple groups were compared. Across-experiment comparisons of memory decay were conducted via a 3-way, mixed-design ANOVA (3 experiments $\times$ 2 groups $\times$ 2 memory types) with repeated measures on memory type. Post hoc [least significant difference (LSD)] tests were performed if necessary to control familywise error. The significance level was set at $\alpha = 0.05$.

RESULTS

Experiment 1: retrieval by motor execution does not induce motor interference. Subjects could learn both perturbations simultaneously when they were presented in a random and interleaved order. Both types of learning appeared to reach a plateau after 20 trials (Fig. 2A). We found no significant difference between the average performance over approximately the 31st to 35th trial and the last 5 trials in the training phase (e.g., for Control Group, $t_{11} = 2.09, 1.98, P > 0.05$ for rotation and gain learning, respectively). In addition, we compared the catch trials with the last 5 trials in the training phase and found no significant difference (e.g., for Control Group, $t_{11} = 2.03, 1.84, P > 0.05$ for rotation and gain learning, respectively). Thus subjects effectively learned 2 visuomotor mappings.

Different groups of subjects also achieved similar levels of learning. Average learning percentages achieved for visuomotor rotation during the last five training trials were 90.7 ± 2.0 (SE, same below), 86.4 ± 2.2 , and $87.3 \pm 1.5\%$ for Control Group, Rotation-Retrieval Group, and Gain-Retrieval Group, respectively. Average learning achieved for visuomotor gain

Fig. 2. Results from *experiment 1* and control experiments. **A**: percentage of learning for visuomotor rotation and gain over trials. The data of Rotation-Retrieval Group, as an example of dual-learning groups, is shown as average $\pm$ SE across subjects (color shades); the data of 2 single-learning groups (control experiments) is only shown as average over subjects. For dual-learning groups, both types of memory are largely intact with small decay during retest. **B**: the memory of rotation learning before and after extra training for all groups. **C**: the memory of gain learning, plotted in the same format as in **B**. **D**: the amount of memory decay for each group, plotted separately for rotation and gain learning. Error bars represent SE for each group. n.s., Not significant.



was 97.3 ± 1.4 , 98.0 ± 1.9 , and $94.3 \pm 2.0\%$ for these groups. Importantly, one-way ANOVA revealed that there was no significant difference between groups [$F_{(2,33)} = 1.40$, 1.22 , $P = 0.26$, 0.31 for rotation memory and gain memory, respectively]. In other words, all groups achieved similar baseline learning before the retrieval (Fig. 2, *B* and *C*). These learning percentages were on par with those reported in the literature for learning a single visuomotor mapping (Pine et al. 1996).

Indeed, learning of a single mapping was similar to simultaneously learning of two mappings. For single-learning groups in our control experiments, the average learning percentages achieved during the last five training trials were 90.8 ± 2.9 and $98.4 \pm 1.9\%$ for visuomotor rotation and gain, respectively. These learning levels were not statistically different from those achieved in dual-learning groups. For example, compared with Rotation-Retrieval Group (the group shown in Fig. 2*A*), there was no significant difference between groups ($t_{18} = 1.24$, 0.14 , $P > 0.05$ for rotation and gain learning, respectively). In terms of learning rate, we identified the first trial that was not statistically different from the average of the last five trials (learning plateau). This trial was regarded as the time when subjects successfully learned the mapping if its next trial was also not statistically different from the learning plateau. For dual-learning groups (e.g., the Rotation-Retrieval Group), the learning was achieved at the 7th and 12th trial for rotation and gain, respectively. For single-learning groups, it was achieved at the 7th and 8th trial, respectively. Thus the learning rates between single-learning groups and dual-learning groups are quite similar. These results indicate that subjects were able to learn simultaneously two distinct visuomotor mappings as adequately as they learn each of the mappings alone. We used the average performance of the last five training trials to quantify the achieved learning in the subsequent analyses.

After the retrieval phase (or equivalent idle period in Control Group), all groups exhibited memory decay for both types of learning in the retest phase (Fig. 2). The retention of visuomotor rotation was 76.4 ± 9.8 , 78.1 ± 4.6 , and $68.4 \pm 8.7\%$ for the three groups, respectively (Fig. 2*B*). The retention of visuomotor gain was 81.9 ± 6.3 , 76.9 ± 6.0 , and $75.9 \pm 4.2\%$, respectively (Fig. 2*C*). Importantly, retrieval by execution did not improve the retention of the retrieved memory as group comparisons were not significantly different (P s > 0.05 for all comparisons) nor did it impair the unretrieved memory. These findings were further confirmed by examining the memory decay (i.e., the difference between the end of training and the retest), which was not significantly different across groups (P s > 0.05 for all comparisons; Fig. 2*D*). Taken together, these results suggest that retrieving one motor memory by execution does not impair the recall of another simultaneously learned motor memory.

Experiment 2: visually cued mental rehearsal induces motor interference. Subjects could learn both perturbations simultaneously as described in *experiment 1* (Fig. 3*A*). In Rotation-Retrieval Group, the average learning percentages for rotation and gain at the end of the training phase were 90.6 ± 2.0 and $97.0 \pm 2.6\%$, respectively. In Gain-Retrieval Group, the average learning percentages for rotation and gain after training were 89.9 ± 2.0 and $96.1 \pm 2.3\%$, respectively. We conducted a one-way ANOVA on the learning percentages across the three groups (Control Group, Rotation-Retrieval Group, and Gain-Retrieval Group; we used the same Control Group in *experiment 1*) and found no significant difference [$F_{(2,33)} = 0.05$, 0.08 , $P = 0.96$, 0.92 for rotation and gain memory, respectively]. This suggests that the learning achieved before retrieval was similar across the three groups (Fig. 3, *B* and *C*).

After the retrieval phase (or equivalent idle period), all groups exhibited memory decay (Fig. 3). Importantly, the

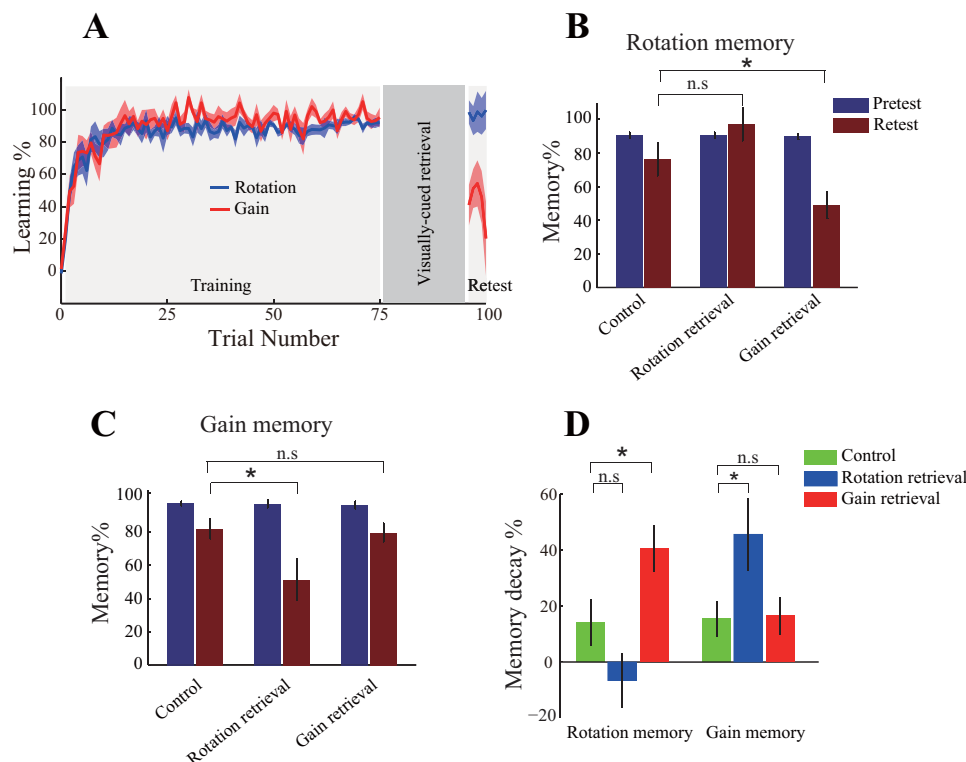


Fig. 3. Results from *experiment 2*. *A*: percentage of learning for visuomotor rotation and gain over trials (only Rotation-Retrieval Group is shown). During the retest, the retrieved memory (rotation) is largely unchanged, whereas the memory of gain learning shows a large decay. *B*: the memory of rotation learning before and after retrieval for all groups. *C*: the memory of gain learning, plotted in the same format as in *B*. *D*: the amount of memory decay for each group, plotted separately for rotation and gain learning. Error bars denote SE for each group. $*P < 0.05$.

decay was dependent on the retrieval. Compared with control subjects, subjects who retrieved rotation learning showed similar retention in rotation learning but significantly less retention in gain learning (comparing the retest performance between Control Group and Rotation-Retrieval Group, $t_{22} = 1.50, 2.14, P = 0.15, < 0.05$ for rotation and gain memory, respectively; Fig. 3, *B* and *C*). Similarly, subjects who retrieved gain learning showed similar retention in gain learning but significantly less retention in rotation learning (Control Group vs. Gain-Retrieval Group, $t_{22} = 2.12, 0.06, P < 0.05, = 0.96$ for rotation and gain memory, respectively; Fig. 3, *B* and *C*). This retrieval-dependent memory decay can be further examined by comparing the amount of memory decay between groups (Fig. 3*D*). Memory decay was significantly different across the three groups [$F_{(2,33)} = 7.33, 3.76, P < 0.01, 0.05$ for rotation and gain memory, respectively]. The memory decay of rotation learning was significantly larger after gain retrieval (Gain-Retrieval Group, $40.7 \pm 8.3\%$; $P < 0.05$, post hoc LSD test) compared with the Control Group ($14.3 \pm 8.3\%$). Similarly, the memory decay of gain learning was about three times larger when subjects retrieved rotation learning (Rotation-Retrieval Group, $45.7 \pm 13.0\%$) compared with the Control Group ($15.4 \pm 6.1\%$; $P < 0.05$, post hoc LSD test). Taken together, these results suggest that retrieving one type of motor memory by mental rehearsal leads to impaired recall of the other type of motor memory.

Experiment 3: retrieval by passive movements induces motor interference. During retrieval, the subject simply relaxed and allowed his/her hand pulled toward targets by the robot. Reaching trajectories of these passive movements were very similar

to those of voluntary movements (Fig. 4*A*). We compared average movement direction, distance, and duration between the last 20 training trials and the 20 passive-movement trials. None of them was significantly different for Rotation-Retrieval Group ($t_{11} = 0.96, 0.32, 0.45, P > 0.05$, respectively; paired t -tests). For Gain-Retrieval Group, there was also no significant difference in terms of average movement direction, distance, and duration ($t_{11} = 1.27, 0.23, 1.07; P > 0.05$, respectively). These results indicated that robot-produced passive movements had similar kinematic profiles as voluntary movements, meeting our goal to provide comparable proprioceptive cues to support conscious retrieval of motor memory.

For learning performance, we first confirmed that subjects in Control Group, Rotation-Retrieval Group, and Gain-Retrieval Group achieved similar learning after training [1-way ANOVA, $F_{(2,33)} = 0.07, 0.12, P = 0.932, 0.887$ for rotation and gain memory, respectively; Fig. 4, *B* and *C*]. After retrieval, all groups exhibited memory decay for both types of learning (Fig. 4). This decay was again dependent on the retrieval. Compared with control subjects, subjects who retrieved rotation learning showed similar retention in rotation learning but significantly less retention in gain learning (for the retest performance, Control Group vs. Rotation-Retrieval Group, $t_{22} = 0.08, 3.00, P = 0.94, < 0.01$ for rotation and gain memory, respectively; Fig. 4, *B* and *C*). Similarly, subjects who retrieved gain learning showed similar performance retention in gain learning but significantly less retention in rotation learning (Control Group vs. Gain-Retrieval Group, $t_{22} = 2.46, 1.02, P < 0.05, = 0.32$ for rotation and gain memory, respectively; Fig. 4, *B* and *C*). This retrieval-depen-

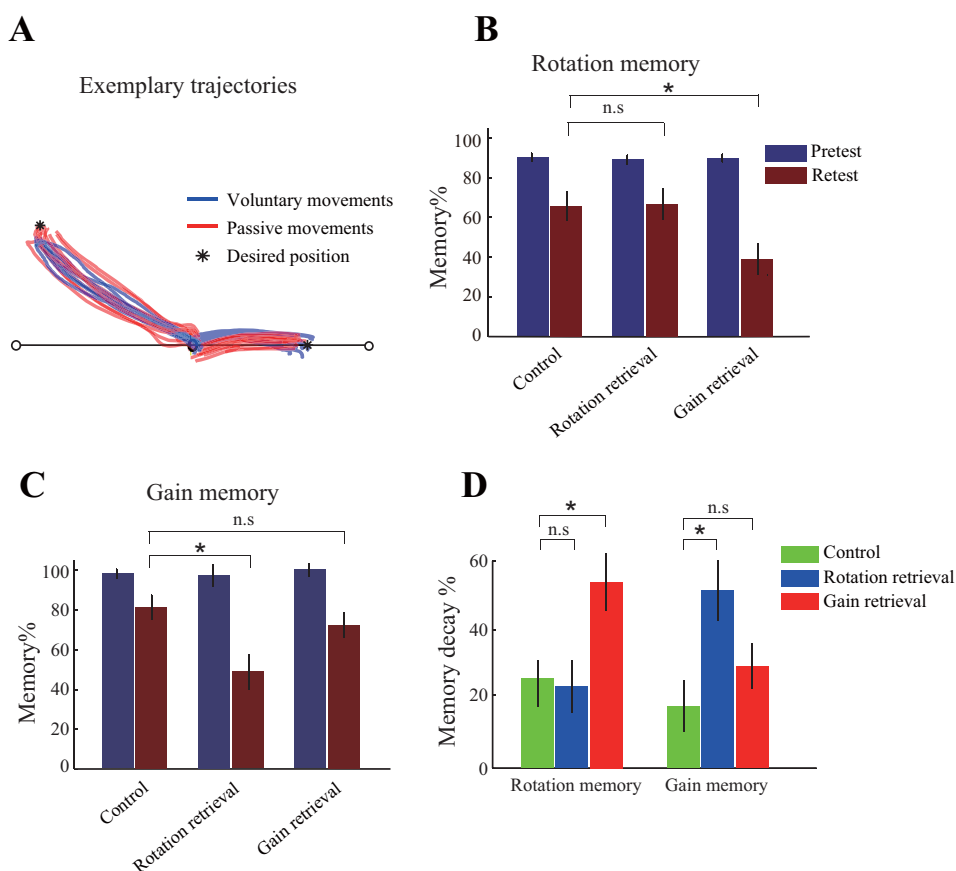


Fig. 4. Results from experiment 3. *A*: reach trajectories for the last 10 training trials and 10 passive-movement trials from 2 typical subjects (trajectories on the left, from Rotation-Retrieval Group; on the right, from Gain-Retrieval Group). *B*: the memory of rotation learning before and after retrieval for all groups. *C*: the memory of gain learning. *D*: the amount of memory decay for each group, plotted separately for rotation and gain learning. Error bars represent SE for each group. * $P < 0.05$.

dent memory decay can be further examined by comparing the amount of memory decay between groups (Fig. 4D). Memory decay was significantly different across the three groups [$F_{(2,33)} = 4.69, 4.96, P < 0.05$ for rotation and gain memory, respectively]. The memory decay of rotation learning was significantly larger after subjects retrieved gain learning (Gain-Retrieval Group, $50.8 \pm 7.9\%$) compared with the Control Group without retrieval ($24.4 \pm 6.8\%$; $P < 0.05$, post hoc LSD test). Similarly, the memory decay of gain learning was significantly larger after subjects retrieved rotation learning (Rotation-Retrieval Group, $48.6 \pm 8.3\%$) compared with the Control Group ($16.9 \pm 7.0\%$; $P < 0.01$, post hoc LSD test). These results thus suggest that retrieving one motor memory with mental rehearsal assisted by passive movements can impair the recall of the other motor memory.

Cross-experiment comparisons. To make direct comparisons of memory decay across the 3 experiments, we performed a 3-way, mixed-design ANOVA (3 experiments $\times$ 2 retrieval groups $\times$ 2 memories). The main effect of the experiment was significant [$F_{(2,66)} = 6.43, P < 0.01$]. Post hoc test revealed that memory decay in *experiment 3* was larger than that in *experiment 1* (37.40 ± 4.16 vs. $16.69 \pm 6.69\%$; $P < 0.01$), possibly owing to the larger memory decay induced by longer retrieval time in *experiment 3* (90 s) than in *experiment 1* (60 s). The main effects of memory and group were not significant [$F_{(2,66)} = 2.77, 1.23, P = 0.10, 0.27$, respectively].

There was a significant two-way interaction of memory and group [$F_{(2,66)} = 31.40, P < 0.001$]. Pairwise comparisons showed that in Rotation-Retrieval Groups the decay of gain memory was larger than that of rotation memory (38.47 vs. 8.01% ; $P < 0.001$), whereas in Gain-Retrieval Groups the decay of rotation memory was larger than that of gain memory (36.82 ± 4.45 vs. $20.30 \pm 4.57\%$; $P < 0.01$). These effects were consistent with the retrieval-specific interference we found in individual experiments.

There was also a significant three-way interaction of experiment, memory, and group [$F_{(4,66)} = 5.02; P < 0.01$]. Pairwise comparisons revealed that for Rotation-Retrieval Groups the decay of gain memory was larger in *experiments 2* and *3* compared with *experiment 1* (P s < 0.05), suggesting that gain memory decayed more with visually cued or robot-assisted mental rehearsal than with motor execution. In terms of rotation memory, there were no differences across experiments (P s > 0.05) except that *experiment 3* has more decay than *experiment 2* ($P < 0.05$). Taken together, after retrieving rotation memory, there was more decay in gain memory with mental rehearsal-related experiments.

For Gain-Retrieval Groups, the decay of rotation memory was larger for *experiment 2* ($P < 0.05$) and *experiment 3* ($P < 0.01$) compared with *experiment 1*, suggesting that rotation memory decayed more with visually cued or robot-assisted mental rehearsal than with motor execution. There was no significant difference across the three experiments in terms of gain memory (P s > 0.05). This, again, was consistent with the retrieval-specific interference found in individual experiments.

Taken together, cross-experiment comparisons confirmed that mental rehearsal, compared with further practicing, of one memory leads to more memory decay of the other simultaneously learned memory.

DISCUSSION

In this study, participants were able to learn simultaneously two distinct visuomotor mappings. Crucially, retrieving one motor memory (e.g., visuomotor rotation) by cued mental rehearsal, rather than by motor execution, would impair the immediate recall of the other memory (e.g., visuomotor gain). This interference effect is content-independent as mental rehearsal of either type of visuomotor memory can lead to impaired recall of another type of memory.

A rather intriguing finding here is that conscious retrieval, instead of execution, can cause immediate interference effect for simultaneously learned motor memories. We argue that this might be related to distinct functional features and neural activations associated with mental rehearsal. Mental rehearsal, often called motor imagery, is defined as conscious rehearsal of motor acts in the working memory without overt movements (Solodkin et al. 2004). Despite large functional equivalence between motor execution and motor imagery, especially for the phase of motor preparation (Decety et al. 1994; Grafton et al. 1996; Grezes and Decety 2001; Stephan et al. 1995), there are also distinct functional differences between the two: motor preparation is an entirely nonconscious process, whereas motor imagery inevitably involves conscious access to images (Annett 1995; Jackson et al. 2003; Jeannerod 1994). Furthermore, motor preparation is usually brief, whereas motor imagery involves prolonged attentional processing associated with executive control, working memory, and response preparation (Decety 1996). More importantly, converging evidence indicates that motor imagery, compared with corresponding motor execution, involves more activations in neural circuits responsible for motor planning and response selection. These areas include prefrontal (Jeannerod 2001), precentral sulcus/middle frontal gyrus (Hanakawa et al. 2003), supplementary motor areas (Gerardin et al. 2000; Hanakawa et al. 2008), left posterior parietal areas (Gerardin et al. 2000; Hanakawa et al. 2003), precuneus (Hanakawa et al. 2003), and basal ganglia (Gerardin et al. 2000; Jeannerod 2001). Among them, prefrontal cortex, supplementary motor areas, and basal ganglia are specifically involved to select appropriate motor plans and to reject the irrelevant ones (Decety 1996; Jeannerod 1994, 2001). Therefore, it is reasonable to assume that retrieving one motor memory during mental rehearsal involves inhibition of a competing memory, and this process is more pronounced during motor imagery than during motor execution. This inhibition possibly leads to our observed impairments in immediate recall of unretrieved memory.

The absence of interference with further motor practice might be related to functional stages of motor learning. Brain imaging studies suggest that whereas early learning relies strongly on prefrontal cortex, later learning is associated with increasing activity in subcortical motor regions (Ashby et al. 2010; Doyon and Benali 2005; Floyer-Lea and Matthews 2004). The learning-related shift in activation from anterior to more posterior regions of the brain reflects a gradually reduced reliance on attentional resources and executive function (Dayan and Cohen 2011; Floyer-Lea and Matthews 2005; Lashley 1950). This reduction is especially apparent when repetitively practicing the same movement after learning has reached near-asymptote level (Ashby et al. 2010; Dayan and Cohen 2011; Doyon and Benali 2005; Schneider and Shiffrin

1977). Hence, we speculate that further practicing a sensorimotor map (in *experiment 1*) after initial acquisition involves minimum executive control and response selection, processes governed mostly by prefrontal cortex. This, in turn, lowers the demands for mediating competition between memories. Thus, in contrast to mental rehearsal, active execution of a motor memory, paradoxically, does not impair the recall of another related memory.

In the area of motor learning, interference between tasks is conventionally induced by movement execution (Krakauer et al. 1999; Shadmehr and Brashers-Krug 1997; Shadmehr and Holcomb 1997). For instance, to interfere with one recently learned motor memory and examine its consolidation, people are usually required to practice a task with opposite perturbations (Brashers-Krug et al. 1996; Krakauer et al. 2005; Sing and Smith 2010). Our study evidenced that practicing an opposite task is not necessary for inducing interference between tasks and conscious retrieval can be a novel and convenient tool to fulfill this goal. However, whether our retrieval-induced interference is transient or long-lasting as retrograde interference (Brashers-Krug et al. 1996; Miall et al. 2004; Shadmehr and Brashers-Krug 1997) is still an open question.

Mental rehearsal affects the recall of the unretrieved memory, which is remarkably similar to the RIF in the domain of declarative memory. When a memorized word is consciously retrieved, the recall of a related but unretrieved word is impaired (Anderson et al. 1994; Chan 2009; MacLeod et al. 2011; MacLeod and Macrae 2001; Saunders et al. 2009). This parallel between sensorimotor memory and declarative memory has been suggested (Krakauer 2009; Krakauer et al. 2005) but has never been backed up with systematic examination. Our findings provide the first support for this hypothesis. Our results also echo the growing evidence that sensorimotor memory and declarative memory interact with each other and potentially even share common resources (Brown and Robertson 2007a,b; Keisler and Shadmehr 2010). In terms of RIF effect itself, it has been proven to be a highly robust and general phenomenon, emerging in different types of memories, including semantic memory (Anderson et al. 1994; Levy et al. 2007), episodic memory (Ciranni and Shimamura 1999; Garcia-Bajos et al. 2009), and procedural memory (Tempel and Frings 2013). We speculate that working memory plays a central role for eliciting RIF since retrieval inevitably involves working memory, no matter what memory systems are involved. A recent study found that higher working memory capacity led to less RIF effect, in support of this hypothesis (Mall and Morey 2013).

Whether RIF is noninhibitory or inhibitory in nature is an ongoing debate in the realm of declarative memory (Anderson 2003; Perfect et al. 2004; Williams and Zacks 2001). Whereas the inhibitive account argues that the forgetting is a result of active processes directly inhibiting the unretrieved item to resolve the competition, noninhibitive account argues that forgetting is simply a consequence of blocking or strength-based interference caused by increased competition arising from the strengthening of practiced items. Our results argue against the noninhibition account as further practicing of a motor memory does not lead to impaired recall of nonpracticed memory (*experiment 1*); this contradicts the prediction of the noninhibition account.

Our findings indicate that mental rehearsal can have detrimental effects on motor skills if their related, simultaneously

learned memory is retrieved. Interestingly, the prevailing view emphasizes the beneficial effects of mental rehearsal. Mental practice of motor skill usually complements actual training in athletes and during rehabilitation (Lotze and Halsband 2006) or even leads to performance improvements (Yue and Cole 1992). Our results, instead, suggest that in practice we should not neglect its detrimental effect if multiple related motor skills are mentally rehearsed.

The impairment of memory recall might also relate to the choking effect observed in elite athletes (Baumeister 1984; Baumeister and Showers 1986; Kimble and Rezaek 1992). Under pressure, they occasionally falter in performance even though the motor skills have been overlearned and can be performed without working memory (Jordet 2009; Willingham 1998). It has been proposed that attention to the step-by-step procedure disrupts the well-learned, proceduralized performance (Beilock and Carr 2001; Beilock et al. 2002; Jackson et al. 2006; Pijpers et al. 2005). This interpretation is in line with our findings as mental rehearsal in our experiments also demands for attending to movement details, and it, in turn, leads to impairment of memory recall. It also suggests that choking effect could be related to conscious retrieval of motor memory.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

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

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