Behavioral/Systems/Cognitive

Adaptation to Visuomotor Transformations: Consolidation, Interference, and Forgetting

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The paradigm task A→task B→task A, which varies the time interval between task A and task B, has been used extensively to investigate the consolidation of motor memory. Consolidation is defined as resistance to retrograde interference (interference by task B on initial learning of task A). Consolidation has been demonstrated for simple skills, motor sequencing, and learning of force fields. In contrast, evidence to date suggests that visuomotor learning does not consolidate. We have shown previously that adaptation to a 30° screen–cursor rotation is faster and more complete on relearning 24 hr later. This improvement is prevented if a 30° counter-rotation is learned 5 min after the original rotation. Here, we sought to identify conditions under which rotation learning becomes resistant to interference by a counter-rotation. In experiment 1, we found that interference persists even when the counter-rotation is learned 24 hr after the initial rotation. In experiment 2, we removed potential anterograde interference (interference by task B on relearning of task A) by introducing washout blocks before all of the learning blocks. In contrast to experiment 1, we found resistance to interference (i.e., consolidation) when the counter-rotation was learned after 24 hr but not after 5 min. In experiment 3, we doubled the amount of initial rotation learning and found resistance to interference even after 5 min. Our results suggest that persistent interference is attributable to anterograde effects on memory retrieval. When anterograde effects are removed, rotation learning consolidates both over time and with increased initial training.

Key words: **motor learning; consolidation; retrograde interference; anterograde interference; visuomotor rotation; arm movements**

Introduction

A seminal study by Shadmehr and Brashers-Krug (1997) demonstrated that adaptation to a rotatory viscous force field during reaching movements is more rapid and complete when subjects are reexposed to the same field after an interval of hours or days. However, the improvement on retest did not occur if, after learning the first force field, subjects adapted to a second force field that rotated in the contrary direction. Importantly, these authors found that the second task no longer interfered with the relearning of the first task if sufficient time (i.e., >5.5 hr) elapsed between the two tasks. These findings led to two important conclusions. First, motor memory, like declarative memory, undergoes a process of consolidation whereby one newly acquired internal model for feedforward control becomes increasingly resistant to interference by a competing internal model simply as a function of time. Second, the interference mechanism is retrograde, not anterograde. Interference is retrograde when task B interferes with the previous learning of task A. Interference is anterograde when task B interferes with the relearning of task A. Anterograde interference, unlike retrograde interference, should not be affected by the interval between tasks A and B.

Subsequent studies have shown that interference also occurs for visuomotor learning: faster and more complete relearning is prevented if subjects learn a conflicting motor task shortly after original learning (Krakauer et al., 1999; Bock et al., 2001; Tong et al., 2002; Wigmore et al., 2002). However, a recent study argues that interference with visuomotor learning is mediated by anterograde, not retrograde, mechanisms (Miall et al., 2004), which is consistent with the fact that previous studies of visuomotor learning have been unable to demonstrate resistance to interference with the passage of time (Bock et al., 2001; Goedert and Willingham, 2002). Thus, unlike for the learning of dynamics, it remains uncertain whether memory stabilization occurs for visuomotor learning.

Here, we sought to address the discrepancy, with regard to consolidation, between visuomotor and other forms of motor learning through a series of experiments examining adaptation to a 30° visuomotor rotation and the effects of a 30° counter-rotation on relearning 24 hr, 48 hr, or 1 week later. First, we asked whether the interfering effect of counter-rotation training on relearning of the original rotation is reduced when counter-rotation training is delayed, as predicted by the consolidation hypothesis. This did not occur, but our analysis suggested that the anterograde effects of counter-rotation training could have masked a consolidation process. Therefore, in a second experiment, we modified the experimental protocol, adding blocks of

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Table 1. Experimental conditions

	Learning rotation	Learning counter-rotation	Relearning rotation
Experiment 1			
Group 1 (6 subjects)	B, B, R		R (1 week)
Group 2 (6 subjects)	B, B, R	CR (5 min)	R (1 week)
Group 3 (6 subjects)	B, B, R	CR (2.5 h)	R (1 week)
Group 4 (6 subjects)	B, B, R	CR (24 h)	R (1 week)
Experiment 2			
Group 5 (6 subjects)	B, B, R		B, R (48 h)
Group 6 (6 subjects)	B, B, R	B, CR (5 min)	B, R (48h)
Group 7 (6 subjects)	B, B, R	B, CR (24 h)	B, R (48 h)
Experiment 3			
Group 8 (6 subjects)	B, B, R, B, R		B, R (48 h)
Group 9 (6 subjects)	B, B, R, B, R	B, CR (5 min)	B, R (48 h)
Group 10 (6 subjects)	B, B, R, B, R	B, CR (24 h)	B, R (48 h)
Group 11 (3 subjects)	B, B, R, B, R	B, CR, B, CR (5 min)	B, R (48 h)
Group 12 (3 subjects)	B, B, R, R	B, CR (5 min)	B, R (48 h)
Experiment 4			
Group 13 (6 subjects)	B, B, R		B, R (24 h)
Group 14 (6 subjects)	B, B, R		B, R (24 h)

B, Baseline; R, rotation; CR, counter-rotation.

trials with no rotation to "washout" aftereffects introduced by the counter-rotation, before assessing changes in performance on relearning of the original rotation. In a third experiment, we asked whether more prolonged learning on day 1 induces greater resistance to interference by a counter-rotation. Finally, we examined whether the degree of improvement seen at relearning diminishes over time.

These results have been presented previously in abstract form (Krakauer et al., 2003).

Materials and Methods

Subjects. Seventy-eight right-handed subjects (46 men, 32 women, 24–40 years of age) participated in the study. All of the subjects were naive to the purpose of the experiments, signed an institutionally approved consent form, and were paid to participate. There were four experiments, and subjects were randomly assigned to a particular group within each experiment (14 groups in total) (Table 1).

General experimental procedure. The setup was similar to one described in detail in previous reports (Ghilardi et al., 2000; Krakauer et al., 2000). Subjects sat facing a computer monitor and controlled a screen cursor by moving a hand-held indicator across the surface of a horizontal digitizing tablet (sampling rate, 200 Hz) with their right arm. An opaque shield prevented subjects from seeing their hand or arm. The target set consisted of eight radially arrayed circles, separated by 45°, placed 4.2 cm from a central starting point, and displayed on a computer monitor. These targets were presented at a regular rate of 1 per second concurrently with a go-tone. For each cycle, the eight targets were presented in a pseudorandom order. Subjects were instructed to make straight out-and-back movements, to reverse direction sharply within the target, and to move as fast as possible without trajectory corrections. The cursor location was visible on the screen at all times. Targets were presented in blocks of 11 cycles of 8 targets resulting in 88 movements per block. Subjects were given 30 sec to rest between blocks.

Experimental sessions were run across 2 or 3 d, separated by 24 hr, 48 hr, or 1 week, depending on the experiment (see below). On the first day, all of the subjects first experienced two baseline blocks, the first of which served to familiarize subjects with the task and the apparatus, in which hand movements were mapped normally to the motions of the screen cursor (right–left were the same for screen and hand; forward–backward motions of the hand were up and down on the screen). Subsequently, subjects performed three or more training blocks of rotation in which the screen cursor was rotated 30° counterclockwise around the center of the start location. Then, after a variable delay interval, certain subgroups of subjects performed three or more interference blocks of counter-rotation in which the cursor was rotated 30° clockwise. On a subsequent day, subjects relearned three blocks of the 30° rotation. In some experiments, subjects performed an additional baseline block before counter-rotation learning and rotation relearning (details for each of the four experiments are provided in Table 1).

Data analysis. For each movement, peak velocity and reversal points were calculated as reported previously (Ghilardi et al., 2000; Krakauer et al., 2000). We used the initial directional error as the measure of rotation adaptation. This was calculated as the difference between the direction of the target from the initial hand position and the direction of the hand at the peak outward velocity from the initial hand position. To assess the time course of adaptation to the imposed rotations, we computed the mean directional error over successive cycles of eight movements. To adjust for small intersubject differences in baseline directional biases (Ghilardi et al., 1995), the directional error of movements performed during the rotation task was corrected by subtracting the corresponding value of the mean bias during the second baseline block.

In previous publications (Krakauer et al., 1999, 2000; Ghilardi et al., 2000), we found that the time course of error reduction showed an initial rapid change within the first 11 cycles, followed by a slower decline that was well fit by a double-exponential function. To capture the initial rapid rate of learning, we computed the mean percentage of error over cycles 2–11 and then performed a repeated-measures ANOVA to compare initial learning and relearning. Differences between groups were assessed by comparing percentage change in adaptation across sessions with ANOVA, and *post hoc* tests (Bonferroni–Dunn) were considered significant at $p < 0.05$.

Results

Experiment 1: persistence of interference

To determine whether interference, by counter-rotation training, with relearning a rotation is attenuated over time, we compared changes in learning in four groups of six subjects each (Table 1, groups 1–4). On day 1, after two blocks of baseline, all of the subjects learned three blocks of 30° rotation and then relearned three blocks of the same rotation 1 week later. One group served as the control (group 1), one group learned a counter-rotation after 5 min (group 2), one group learned a counter-rotation after 2.5 hr (group 3), and one group learned a counter-rotation after 24 hr (group 4). Figure 1*A*, with grouped data across subjects, shows that directional errors of equal magnitude to the imposed rotation were present during the first cycle of movements on day 1. These errors were initially reduced rapidly within the first 11 cycles and thereafter were reduced more slowly. Relearning 1 week later was considerably more rapid, and the errors made in the first cycle were smaller than on initial exposure.

These differences between learning and relearning were not apparent in the groups that learned the counter-rotation at 5 min, 2.5 hr, or 24 hr (Fig. 1*B–D*). Figure 2*E* shows the percentage change from initial learning (Fig. 1*A–D*, boxed cycles 2–11) in the four groups. There was a large change in the control group, corresponding to an improvement on relearning, which was significantly different from the minimal change in the other three groups. As the time interval between rotation and counter-rotation learning increased, there was a trend toward increased interference, which would not be expected for a consolidation process. To exclude the possibility that learning of the counter-rotation itself might have varied with the time separating it from the original rotation, we computed the amount of learning achieved during the counter-rotation. The mean error in the last two cycles during counter-rotation training was not different across the three interference groups (groups 2–4) ($p > 0.05$) and was also not significantly different from the amount of rotation learning achieved on day 1. Thus, even 24 hr after initial rotation learning, counter-rotation learning prevented improved relearning of the initial rotation 1 week later.

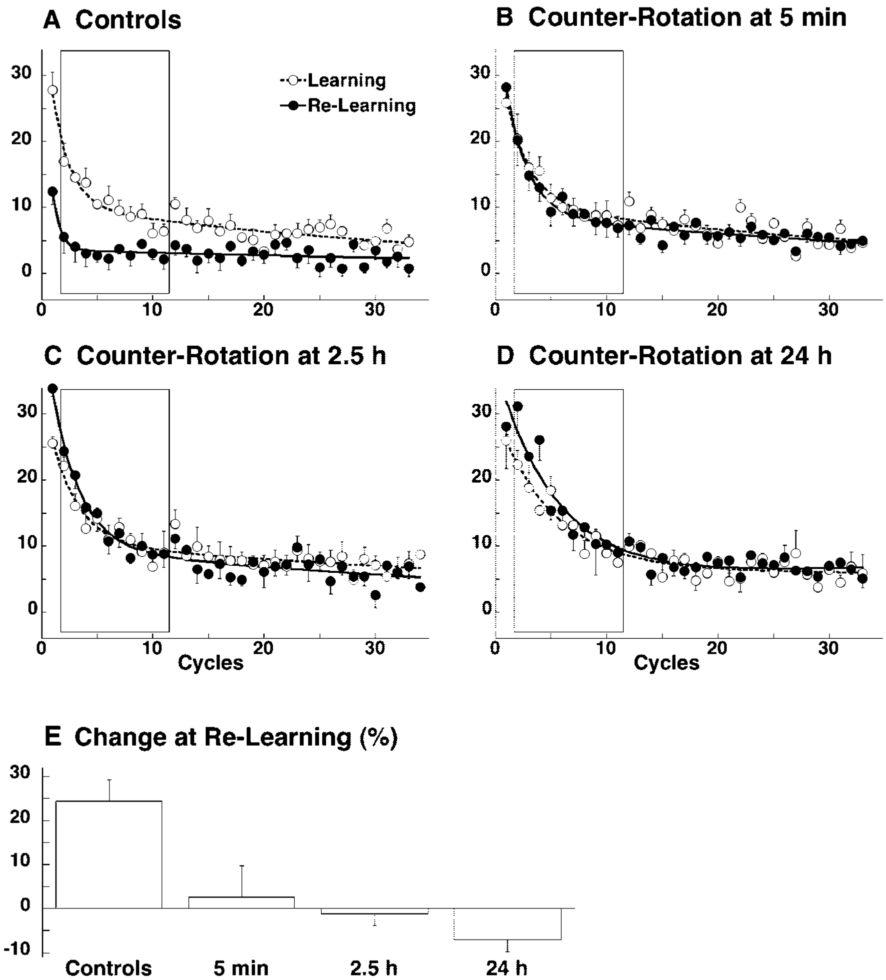

Figure 1. Experiment 1. *A–D*, Rotation learning (open circles and dashed lines) and relearning (filled circles and solid lines) curves for groups 1–4, respectively. Learning is shown by the progressive reduction in the directional error at peak velocity (in degrees) across cycles. Points, representing the group average with SE for each cycle, are fitted by a double-exponential function. Cycles 2–11, which were used in the analysis, are enclosed by a box. Repeated-measures ANOVA showed no main effect of session (learning vs relearning) on directional error ($F_{(1,40)} = 1.13$; $p > 0.05$). However, there was a significant difference between groups ($F_{(3,40)} = 15.54$; $p < 0.0001$) and a significant session × group interaction ($F_{(3,40)} = 5.97$; $p < 0.0018$). This interaction was driven entirely by the control group (group 1), which showed a substantial decrease of directional error with relearning. *E*, Percentage change in rotation learning from the learning to the relearning session. Bars represent mean percentage change and SE for each group. ANOVA revealed an effect of group ($F_{(3,20)} = 9.10$; $p = 0.0005$), and *post hoc* tests showed significant differences ($p < 0.0083$) between the control group and the other three groups but not among the other three groups.

To evaluate whether aftereffects from counter-rotation training contributed to the apparent interference, we compared the directional error in the first cycle of movements for the learning and relearning sessions. Although there was no significant effect of session ($F_{(1,40)} = 0.048$; $p > 0.05$), there was a significant session by group interaction ($F_{(3,40)} = 17.96$; $p < 0.0001$). *Post hoc* tests revealed that only the difference between session 1 and session 2 in the control group was significant. It should also be added that the first cycle of the control group on session 1 was not significantly different from the first cycle of session 2 for the three interference groups. Thus persistence of aftereffects was not the cause of the observed interference, but the results are consistent with some form of interval-independent anterograde mechanism.

Experiment 2: washout unmasks resistance to interference

To prevent anterograde effects as observed in experiment 1, we added two blocks of baseline trials as a washout before relearning in three groups of subjects (Table 1, groups 5–7). After two baseline blocks, these subjects first learned the 30° rotation over three blocks of trials (33 cycles) and relearned the rotation 48 hr later. Group 5 was the control. Groups 6 and 7 learned the counter-rotation 5 min and 24 hr after the original rotation, respectively. In the three groups, the mean directional error at the end of the washout blocks was similar to that at the end of second baseline block (last two cycles, 0.99 ± 2.2 vs −0.06 ± 2.1°; $F_{(2,17)} = 2.2$; $p > 0.5$). This indicates that washout successfully returned subjects to baseline performance.

Compared with learning, relearning was faster, and mean directional errors were lower in all three of the groups (Fig. 2). However, the amount of improvement differed across the three groups and was lowest in the 5 min interference group (group 6) (Fig. 2*D*). There was a significant difference between groups 5 and 6 ($p < 0.016$) but no significant difference between groups 5 and 7 ($p > 0.05$). Thus, by 24 hr, the counter-rotation no longer interfered, consistent with the hypothesis that learning had undergone consolidation during this interval. Of note, in the control group, the directional error for the first cycle was not different on first and second exposures to the 30° rotation (29.3 ± 1.2 vs 26.8 ± 1.0°; $F_{(1,30)} = 2.6$; $p > 0.5$). Therefore, the anterograde effects seen in the control group of experiment 1 did not occur with washout in experiment 2.

Overall, the results of experiment 2 are consistent with retrograde interference and consolidation. In addition, group 6 (interference at 5 min) showed submaximal improvement, which suggests that facilitation and retrograde interference can occur simultaneously.

Experiment 3: increased training reduces susceptibility to interference

This experiment examined whether susceptibility to interference is reduced by increases in initial training. Three groups of six subjects each (Table 1, groups 8–10) were trained on day 1 with six instead of three blocks, comprising 66 cycles of rotation. They relearned three blocks of rotation 48 hr later. The six blocks were separated into three blocks and separated by a single block (11 cycles) of baseline conditions without rotation. Groups 9 and 10 were then given counter-rotation training 5 min and 24 hr, respectively, after the rotation. On day 2, subjects performed two washout blocks without rotation before relearning rotation adaptation.

As shown in Figure 3*A–C*, relearning was faster than initial learning for all three of the groups. However, the amount of improvement, unlike in experiment 2, was the same in all three of the groups and was comparable in magnitude with that seen for relearning in the control group (group 5) and the 24 hr interference group (group 7) in experiment 2 (Fig. 3*D*). Thus, after a longer duration of rotation training, subsequent counter-rotation no longer interfered with improvement on relearning. Resistance to interference was not, however, associated with any change in the amount of adaptation achieved on day 1: the residual directional error in the last two of the 66 cycles of training (4.5 ± 1.99°) was not significantly different from that achieved for the last two of the 33 cycles of training (4.9 ± 3.4°; $F_{(1,36)} = 0.231$; $p > 0.05$) in experiment 2.

It might be argued that the apparent resistance to interference was attributable to the disproportionate amount of learning of the rotation relative to the counter-rotation (66 vs 33 cycles). To examine this possibility, we tested a group of three subjects (group 11) with 66 cycles of counter-rotation 5 min after training with 66 cycles of rotation. The average improvement with relearning (17.5 ± 2.2%) was not less than that for group 9 (17.1 ± 3.3%), which only had 33 cycles of counter-rotation training. Finally, we asked whether it is the spacing of the two blocks of training with a washout block in-between that induces resistance to interference. To address this question, three extra subjects (group 12) were trained with 66 uninterrupted cycles of rotation, followed by 33 cycles of counter-rotation at 5 min. Their average improvement at relearning was 16.89 ± 3.5%. A comparison of groups 9, 11, and 12 showed no significant difference in improvement at relearning ($F_{(2,9)} = 0.197$; $p > 0.05$).

Experiment 4: improvement with relearning decreases with time: forgetting

To assess persistence of improved learning over time, we trained two groups of six subjects (Table 1, groups 13 and 14), one with 33 cycles and the other with 66 cycles of the rotation. Relearning after an interval of 24 hr (group 13, 26.0 ± 4.1°; group 14, 28.30 ± 3.8°) was greater than that for the comparable groups that relearned after 48 hr (group 5, 21.1 ± 2.5°; group 8, 18.36 ± 2.38°; $p < 0.05$). Thus, performance improvement, although still robust at 48 hr, had modestly decayed or previous learning was less retrievable.

Discussion

The experiments presented here sought to determine whether the learning of a visuomotor transformation, specifically a 30° rotation, undergoes a process of consolidation whereby learning becomes resistant to interference. In the first experiment, we found that interference with the 30° rotation by a 30° counter-rotation persisted

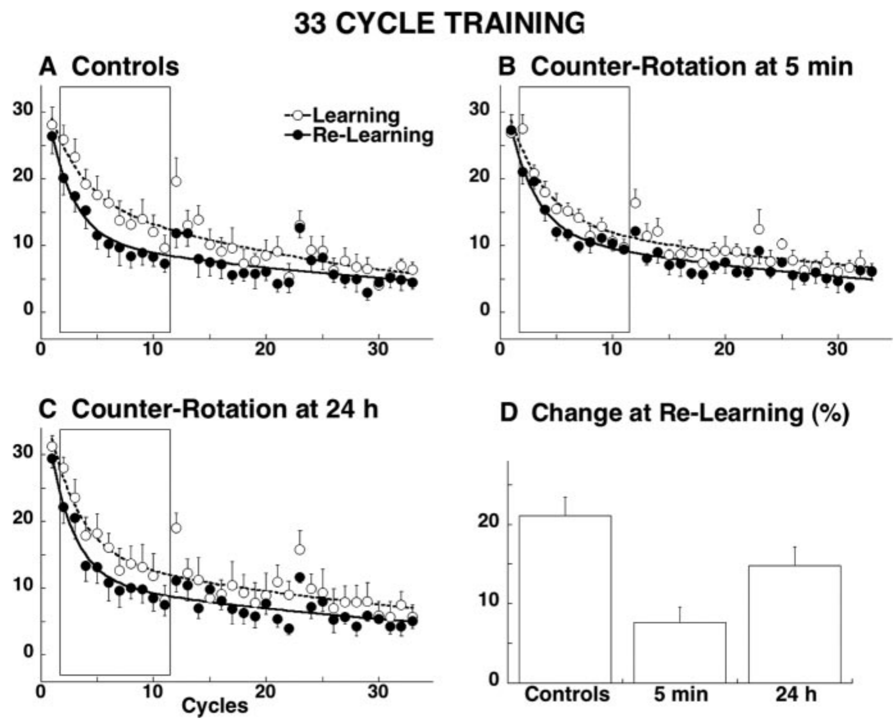

Figure 2. Experiment 2. *A–C*, Rotation learning and relearning curves with washout. Repeated-measures ANOVA revealed a significant effect of session (learning vs relearning) on directional error ($F_{(1,30)} = 10.828$; $p = 0.0026$). There was no significant effect of group ($F_{(1,30)} = 0.097$; $p = 0.9075$) nor a significant session × group interaction ($F_{(3,30)} = 0.439$; $p = 0.649$). *D*, Percentage change in learning from the learning to the relearning session. ANOVA revealed a main effect of group ($F_{(2,15)} = 4.17$; $p = 0.03$). *Post hoc* tests showed a significant difference ($p < 0.016$) between the control and the 5 min interference group but not between the control group and the 24 hr interference group ($p > 0.05$).

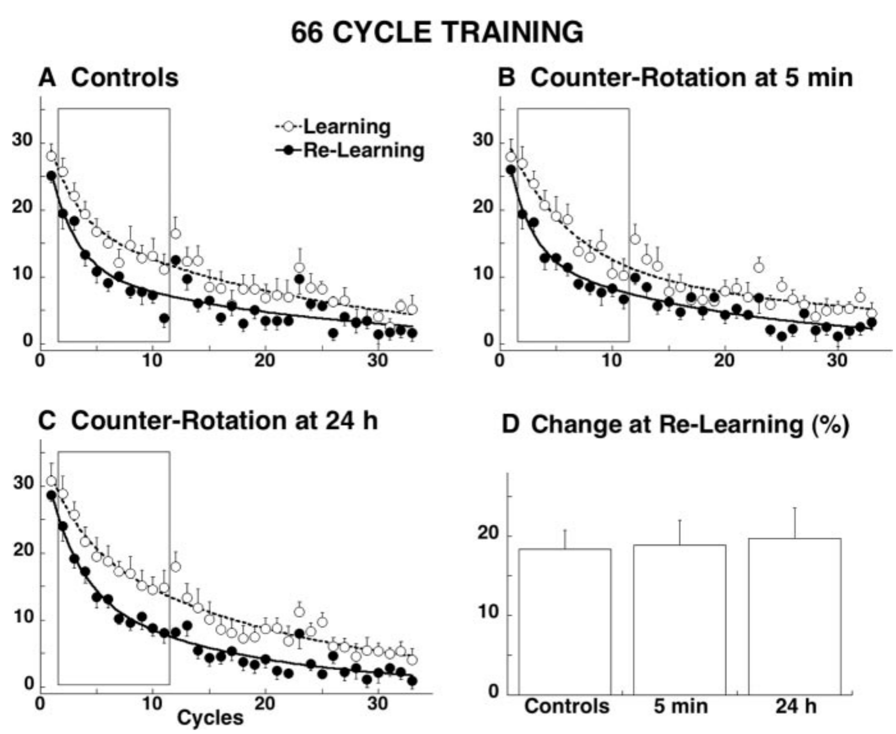

Figure 3. Experiment 3. *A–C*, Rotation learning and relearning curves with extended training and washout. Repeated-measures ANOVA revealed a significant effect of session (learning vs relearning) on directional error ($F_{(1,30)} = 21.16$; $p < 0.0001$). There was no significant effect of group ($F_{(2,30)} = 1.87$; $p = 0.17$) nor a significant session × group interaction ($F_{(3,30)} = 0.009$; $p = 0.99$). *D*, Percentage change in rotation learning from the learning to the relearning session. ANOVA revealed no significant difference between groups ($F_{(2,15)} = 0.046$; $p = 0.95$).

even when adaptation to the counter-rotation occurred a full 24 hr later. This result is consistent with the position that consolidation does not occur for kinematic transformations (Bock et al., 2001; Goedert and Willingham, 2002; Miall et al., 2004; Robertson et al., 2004). However, in experiment 2, when we introduced washout blocks between rotations, resistance to interference was seen after 24 hr but not after 5 min. In our third experiment, when we doubled the amount of initial rotation training, we found resistance to interference by a counter-rotation even at 5 min. These results show that consolidation, defined as resistance to retrograde interference, does occur for kinematic transformations.

Since the reports by Brashers-Krug and Shadmehr (Brashers-Krug et al., 1996; Shadmehr and Brashers-Krug, 1997), which revealed consolidation of force-field learning, attempts to replicate this finding for visuomotor adaptation have been unsuccessful (Bock et al., 2001; Goedert and Willingham, 2002). Indeed, a recent review states the following: "so far, there is no convincing evidence that skill acquired in kinematic adaptation tasks needs to undergo stabilization" (Robertson et al., 2004). Instead, it has been suggested that changes in the time course of adaptation with successive visuomotor rotations simply reflect repeated recalibrations of a single learned reference system (Bock et al., 2003). In this framework, the recalibration process depends on the carryover of aftereffects across conditions. However, our findings are not compatible with this notion, because aftereffects did not persist in experiment 1 and were washed out in experiments 2 and 3. Nevertheless, in experiment 1, we found anterograde interference despite the absence of aftereffects, and, in experiment 2, we found that counter-rotation interferes retrograde with consolidation.

In the original consolidation experiment by Shadmehr and Brashers-Krug (1997), subjects performed ~20 movements in the baseline condition (null field) before relearning the original force field. In contrast, subsequent experiments that have failed to show consolidation did not washout anterograde effects of the interference task. For example, Bock et al. (2001) used a joystick task that introduced sensorimotor discordance. They did not introduce washout blocks and found interference even when the two conflicting tasks were separated by 1 month. In a study of prism adaptation (Goedert and Willingham, 2002), which also did not use washout blocks, an interference effect was present that, if anything, became more pronounced as the interval between the conflicting prism tasks increased from 5 min to 24 hr. This is the opposite of what would be expected for retrograde interference and a consolidation process. Our results from experiment 1 are consistent with these findings: we also found a trend toward increased interference as the interval between initial training and the interference task increased.

In experiment 2, we introduced a baseline block before both counter-rotation and relearning. With this washout, the degree of improvement on relearning was less in the 5 min interference group than in the control and the 24 hr interference groups. There was no significant difference between the control group and the 24 hr interference group. Thus, after 24 hr, the counter-rotation no longer reduced improvement on second exposure to the original rotation. These results indicate that rotation adaptation, in the setting of washout, does show time interval-dependent resistance to interference, consistent with a consolidation process. It has been argued recently that the anterograde effect of the counter-rotation masks observable improvement in relearning of the rotation (Miall et al., 2004). Interestingly, we did see improvement at 5 min, but this was significantly less than in the control and 24 hr groups. Thus, facilitation and retrograde interference can occur simultaneously.

A recent study (Caithness et al., 2004) was unable to replicate our finding that washout of anterograde effects unmasks consolidation of rotation learning (Krakauer et al., 2003). However, in contrast to our control group in experiment 2, their control group did not show significant improvement on relearning. A persistent interference effect of the counter-rotation cannot be inferred when even the control group does not significantly improve at relearning. A possible explanation for the absence of improvement in their study is that, on day 1, despite exposure to a 30° rotation, subjects showed only a 20° error in the first learning block. Thus, lack of improved relearning may have been a result of atypically fast learning on day 1.

The effect of washout blocks leads us to hypothesize that memory for rotation learning was in fact retained in experiment 1, but retrieval was prevented by the counter-rotation. Absence of a retrograde gradient over hours and days has been described in the declarative memory literature for paired-associates word learning (for review, see Wixted, 2004). The explanation given for this phenomenon and supported by experimental data (Anderson et al., 2000; MacLeod and Macrae, 2001) is temporary inhibition of retrieval rather than prevention of consolidation. In this framework, the association of the task context with the last rotation experienced (i.e., the counter-rotation) prevents retrieval of the consolidated memory of the original rotation. In contrast, when subjects are returned to baseline, they are better able to relearn the appropriate rotation, perhaps because the counter-rotation is reduced in salience. The difficulty in distinguishing between a failure to consolidate and a failure to retrieve a consolidated memory remains a subject of considerable debate in the declarative memory literature (Miller and Matzel, 2000; Millin et al., 2001; Dudai, 2004; Hoz et al., 2004). Thus, it is possible that the persistence of interference in experiment 1, and in other experiments like it, is caused by an anterograde effect that masks ongoing consolidation.

We showed resistance to interference, even at 5 min, with an increase in initial training from 33 to 66 cycles. The result cannot be explained by the fact that subjects were trained on twice the number of cycles of the rotation compared with the counter-rotation, because doubling the number of cycles of the latter did not change the result. We also found that it was not the spacing per se of the 66 cycles of training into two blocks of 33 cycles, with a washout in-between, that led to resistance to interference because we saw the same effect with 66 cycles of rotation training without spacing. Of course, this result does not preclude the possibility that other spacing protocols for training would increase resistance to retrograde interference. Finally, the effect of 66 cycles of training was not caused by greater overall adaptation, because this was not different for 33 and 66 cycles of training but instead to more time in the adapted state. A similar relationship of consolidation to the strength of initial learning is described for other forms of learning (Hauptmann and Karni, 2002).

Finally, we found that control subjects who relearned the 30° rotation at 48 hr showed reduced adaptation improvement compared with those who relearned at 24 hr. Thus, motor memory, even when consolidated, either decays or is less well retrieved over time. The latter mechanism is suggested by the control group in experiment 1, which showed the greatest improvement of any group despite an interval of 1 week. This suggests that, although washout blocks reduce anterograde interference by the counter-rotation, they also reduce facilitatory effects of the initial rotation (Bock et al., 2001).

Conclusions

Our results show that consolidation, defined as resistance to retrograde interference, can occur for kinematic transformations, both through a graded effect of time interval and with increased initial training. The persistence of interference across long intervals, as described in previous studies and as we found in experiment 1, is not definitive proof of erasure of initial learning. We suggest instead that the initial rotation is in fact consolidated, but retrieval is prevented by the anterograde effect of counter-rotation. Anterograde interference is mitigated if subjects are returned to baseline between exposures to opposing kinematic transformations, as we did in experiments 2 and 3 and as was done by Shadmehr and Brashers-Krug (1997) in their force-field experiment. A shorter washout period may be sufficient with force-field learning because proprioception may provide a more salient contextual cue. This is suggested by our previous study of the retrieval of novel inertial dynamics: subjects were able to retrieve the learning from the previous days within one cycle of exposure (Krakauer et al., 1999). Additional experiments will be needed to characterize those conditions that interfere with retrieval versus those that interfere with consolidation of motor memories. Finally, our findings of reduced improvement with an increase in the interval to relearning from 24 to 48 hr may explain why athletes practice daily rather than at longer intervals.

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