REACTIVATION PROTECTS HUMAN MOTOR MEMORIES AGAINST INTERFERENCE FROM COMPETING INPUTS

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ABSTRACT

Many newly encoded memories are labile when acquired but then consolidate to more stable states. Reconsolidation theory posits that reactivating a consolidated memory again destabilizes it, increasing its vulnerability to interference from competing memories. In a series of 3-day experiments, we investigated the fate of a motor memory when it is reactivated and challenged with a competing one. We pursued a modular design in which humans adapted to a visuomotor rotation A (day 1), then an opposite rotation B (day 2), followed by a retest on A (day 3). We first found that reactivating A before learning B (A-AB-A) caused no greater impairment in A retention than non-reactivation (A-B-A). That is, while interference occurred, it appeared to be uninfluenced by reactivation, contradicting reconsolidation predictions. We then tested an alternate idea, that reactivation might serve to protect the original memory from interference. In subsequent experiments, we introduced no rotation (N) trials either prior to A relearning (A-AB-NA and A-B-NA groups), or immediately after B learning (A-ABN-A and A-BN-A groups). Here, we observed that reactivation served a protective function, but only when B was washed out immediately, preventing its consolidation (A-ABN-A group). Collectively, our results show that reactivation does not necessarily increase the susceptibility of a motor memory to interference but may rather shield it from degradation by competing learning. Our findings align with theories positing memory transitions between active and inactive states, and hold implications for strategies focused on improving memory retention in rehabilitation, sports and skills training.

Keywords: motor learning, memory, consolidation, reactivation, interference

SIGNIFICANCE STATEMENT

Consolidated memories are widely thought to undergo destabilization when reactivated, which then increases their susceptibility to interference from competing inputs. Diverging from this established model, we demonstrate that reactivation, or active retrieval, of a motor memory does not induce vulnerability, but rather protects the original memory from degradation. This protection occurs specifically when the competing learning remains unconsolidated, indicating some temporal constraints on the mechanism. Our findings question reconsolidation theory in motor systems and support an alternative framework in which reactivation promotes memory stability. They also suggest new principles for optimizing skill retention in rehabilitation, athletic training, and skill acquisition, where protecting existing memories is perhaps as critical as forming new ones.

INTRODUCTION

Motor learning is a fundamental process that enables humans to acquire new skills, adapt to changing environments, and improve performance across a wide range of tasks. Central to this process is the progressive development and storage of a motor "memory". Like other memory systems (McGaugh, 2000; Dudai, 2004; Dudai et al., 2015), motor memories are thought to be fragile immediately after acquisition, but stabilize with time (Brashers-Krug et al., 1996; Shadmehr & Brashers-Krug, 1997) and get represented over distributed neural circuits (Doyon & Benali, 2005; Hikosaka et al., 1999, 2002; Nudo et al., 1996). A key signature of such stabilization, or consolidation, is the resistance of a memory to interference from inputs that might compete for the same neural resources. Consolidation, defined as resilience against interference, implies some kind of a fixation or permanence to a memory. That is, a memory, once consolidated, is believed to be unchangeable (Dudai, 2004; Lee, 2009; Nader et al., 2000a). In error-driven motor learning in humans, consolidation is believed to occur over a ~6-hour interval after initial acquisition (Brashers-Krug et al., 1996; Krakauer, 2009; Krakauer et al., 2005; Krakauer & Shadmehr, 2006). Thus, when challenged with a competing motor task after this time duration, the initial memory remains unaffected and is easily retrievable. In fact, components of such memories are believed to be robust even after several months following training (Landi et al., 2011; Yamamoto et al., 2006).

This notion of relative permanence of consolidated memories has however been challenged by an alternate line of work demonstrating that the initially acquired memory can be updated or altered (Dudai, 2006; Elsey et al., 2018; Nader & Hardt, 2009; Sara, 2000; Schiller, 2022). Crucially, such a change requires that the previously consolidated memory be made temporarily labile through reactivation, or active retrieval (Dudai & Eisenberg, 2004; Schlichting & Preston, 2014). Early tests of this "reconsolidation" theory focused on fear conditioning paradigms in the rodent (Nader et al., 2000b) and demonstrated that a consolidated fear memory can be corrupted if the basolateral amygdala is microinfused with "amnesic agents" such as anisomycin immediately after it is brought to a labile state through reactivation. In contrast, when the memory was not reactivated, injection of anisomycin had no effect and the memory was left intact (Nader et al., 2000b). These initial results, replicated numerous times (for reviews, see Besnard et al., 2012; Nader & Einarsson, 2010; Nader & Hardt, 2009), have been extended to other memory systems such as object recognition memory in the rodent (Davis et al., 2010; Winters et al., 2011). In humans too, reactivation-mediated reconsolidation effects have been widely reported for amygdala-dependent memories (for reviews, see Agren, 2014; Hupbach,

2015; Schiller & Phelps, 2011). Within the motor system, reconsolidation effects have been observed in studies of human motor sequence learning. For example, some classic studies (Goedert & Willingham, 2002; Walker et al., 2003) have demonstrated that an existing memory of a motor sequence can be significantly degraded when an opposing, interfering sequence is learned following its reactivation. In sum, across a number of memory domains, reconsolidation appears to destabilize the original memory, and leads to a significant worsening in later performance, a finding confirmed in numerous other studies as well (Chan & LaPaglia, 2013; Gabitov et al., 2017, 2019; Kindt et al., 2009).

Little is known about reactivation-dependent reconsolidation effects in other forms of motor learning such as that driven by errors or by reinforcement. This is not to say that interference effects have not been investigated in these paradigms; they have indeed been extensively probed (Albert et al., 2022; Avraham & Ivry, 2025; Caithness, 2004; Krakauer, 2009; Krakauer et al., 2005; Kumar et al., 2018; Miall et al., 2004). For instance, in a seminal study, Caithness et al. (2004) examined interference effects in error-based motor adaptation by employing the classic “A-B-A” paradigm. They demonstrated robust interference from an opposing task B on the memory of task A, acquired even up to a week prior. Specifically, when participants performed task A the second time, there was no signature of having learned A before, indicating that the intervening B learning had interfered with the previously consolidated A memory. Similar results were obtained by others as well (Krakauer, 2009; Krakauer et al., 2005). Importantly however, in error-based motor learning, these interference effects between an existing memory and a competing memory did not require reactivation of the original memory. That is, there was *no* reactivation of A prior to the acquisition of B, yet robust interference occurred between them.

What is the fate of the initially acquired motor memory if it *is* reactivated and then challenged with a competing memory? Here we addressed this gap in a series of error-based motor adaptation experiments. We first tested the hypothesis that reactivation of a consolidated memory trace destabilizes it, leaving it susceptible to further degradation if an opposing task is subsequently learned. If this is true, then performance on an initially learned task should be much more impaired when a competing task is learned following its reactivation compared to no-reactivation conditions. Contrary to this however, we did not observe worsening upon relearning. While interference did occur, it was no more severe than in conditions where the original memory was not reactivated. This led us to a new but alternate body of research – that

reactivation might *protect* against interference rather than destabilizing the memory trace (Birbaumer, 2010; Gabitov et al., 2017; Herszage et al., 2021; Herszage & Censor, 2017; Lee, 2008, 2009; Nader, 2015; Nader & Hardt, 2009; Schlichting & Preston, 2014). In our second and third experiments, we modified our paradigm to probe a putative benefit from active retrieval. We indeed found a retrieval-mediated benefit, but only when learning from the interfering task was washed out immediately, i.e., when its consolidation was prevented.

Taken together, our results suggest that reactivation of a consolidated motor memory does not necessarily destabilize it in a way that makes it more vulnerable to interference, as predicted by the classic reconsolidation model. Instead, reactivation may serve a protective function, shielding the original memory when challenged by competing learning. This could have implications in sports, performing arts and neurorehabilitation, in which retention of learned actions over time remains a core aim.

METHODS

Participants

We recruited 140 young, right-handed healthy adults (80 males, 60 females, aged 18 to 40 years) across three experiments. Handedness was determined by the Edinburgh Handedness Inventory (Oldfield, 1971). Participants had no self-reported history of neurological or psychiatric illness, brain injury, or addiction. Experiments were conducted after obtaining written informed consent, and the protocol was approved by the ethics committee of the Indian Institute of Technology Gandhinagar.

Experimental Setup and Task

We used a virtual reality setup where participants sat facing a large digitizing tablet (GTCO CalComp) on which they made planar reaching movements from a circular start position (green color, 1.5 cm diameter) to target circles (red color, 1.5 cm diameter) using a hand-held stylus. A high-definition television screen, positioned above the tablet and facing downwards, was used for presenting the start and target positions. To eliminate direct visual feedback of the hand, a semi-silvered mirror was placed between the television and the digitizing tablet. Feedback about hand position was instead made available via a cursor displayed on the screen along with the start position and targets. This cursor feedback could be aligned with the actual hand position or rotated relative to the direction of hand motion (visuomotor rotation).

Participants performed 10 cm long-reaching movements from the start position to the target circle. Each trial began by participants bringing the stylus into the start circle and staying there for 250 ms, after which one of the eight radially arranged targets appeared simultaneously with an audio “go” cue. The order of target presentation was pseudo-randomized such that a target appeared only once per cycle of 8 consecutive trials. Participants were instructed to move as quickly and accurately as possible to the displayed target. Each trial lasted for a maximum of 2 sec, and if the participant exceeded the time limit, that trial was ended. A score based on the spatial accuracy of the reaching movement was displayed on the screen at the end of each trial. Participants received 10 points for accurately bringing the stylus into the target, 5 points if their action ended outside the target but within a 2.5 cm radius of the target's center, and no points for reaches that ended beyond a 2.5 cm radius from the target center. Points were used primarily to maintain participant motivation; they were not analyzed and did not influence the compensation participants received.

We used a three-day “A-B-A” paradigm that involved learning a 30° counterclockwise rotation A on day 1, followed by adaptation to a competing 30° clockwise rotation B with or without reactivation of the previously consolidated learning of A on day 2, and retesting on A on day 3. Participants started each learning phase at roughly similar times of the day to minimize the effects of circadian rhythm and homeostatic factors. Before learning A on day 1, participants performed 48 no-perturbation trials to familiarize themselves with the setup and the task.

Experiment 1: Participants in experiment 1 were randomly assigned to one of three groups. Participants in the A-B-A group learned rotation A over a block of 20 cycles (1 cycle = 8 trials) on day 1, rotation B over 20 cycles on day 2 and were retested on rotation A over 20 cycles on day 3. In contrast, participants in the A-AB-A group learned A on day 1, practiced A again for 3 cycles on day 2 (reactivation) and then learned B immediately thereafter. This was followed by retesting on A on day 3. Participants in the A-A group learned A on day 1 and were retested on A over 20 cycles on day 3 like the other two groups; this group did not learn B on day 2. Each participant made 20 movements to each target during training.

Experiment 2: In experiment 2, we introduced null rotation (N) trials prior to A relearning on day 3 in two new groups. Participants in the A-B-NA group learned A on day 1 (20 cycles), B on day 2 (20 cycles), and were retested on A on day 3 (20 cycles) after performing 6 “washout” cycles.

No rotation was applied on these washout trials. In contrast, participants in the A-AB-NA learned A on day 1 over 20 cycles, reactivated A (3 cycles) and then immediately learned B (20 cycles) on day 2, and were retested on A (20 cycles) on day 3 following 6 cycles of washout trials.

Experiment 3: Our third experiment was similar to experiment 2, except that we introduced the null rotation washout trials immediately after B learning on day 2. Thus, participants in the A-BN-A group learned A on day 1 (20 cycles), learned B (20 cycles) followed by 6 washout cycles on day 2, and were retested on A (20 cycles) on day 3. In contrast, participants in the A-ABN-A first learned A (20 cycles) on day 1. On day 2, they reactivated A over 3 cycles, then learned B (20 cycles) and then performed 6 cycles of no rotation washout trials. This was followed by retesting on A (20 cycles) on day 3.

Data Analysis

We recorded the hand (stylus) and cursor positions for offline analysis. Kinematic data were filtered using a low-pass Butterworth filter with a cutoff frequency of 10 Hz. Velocity was calculated by differentiating position data. Adaptation to the visuomotor rotation was quantified as a reduction of direction error across learning cycles. Direction error was defined as the angle between the line connecting the start and target circles and the line connecting the start circle and hand position at peak velocity. Direction errors were baseline corrected by subtracting the mean direction error on the last two familiarization cycles from all trials. We focused on the direction errors during the early and late phases of learning, which were defined as the mean direction error on the first and last learning cycle respectively.

Across all three experiments, nine participants (no more than two participants in any single group) had to be excluded from the analysis for protocol violations, including a failure to follow experimenter instructions resulting in highly aberrant movements during A learning on day 1. For the remaining 131 participants, trials where they did not move, or start a trial within the stipulated time, or lifted the stylus off the tablet leading to a loss of data, were labeled as “bad trials” and omitted. In addition, trials where direction errors were more than 3 standard deviations away from the mean direction error computed for each learning phase within each group were treated as outliers and excluded. Across all participants included in the final analysis (n = 58 for experiment 1, 37 for experiment 2 and 36 for experiment 3), a total of 1.3% of trials were removed based on all of the above criteria combined. The details of the statistical tests

used for comparing the different groups are provided along with the corresponding results. The significance threshold for all comparisons was set at 0.05.

RESULTS

Interference was not influenced by reactivation

Participants were divided into three groups: participants in the A-AB-A group (n = 19) briefly reactivated A on day 2, while those in the A-B-A (n = 19) did not. The third, A-A group (n = 20) served as the control wherein participants did not learn the interfering task B on day 2. All groups relearned A on day 3.

Figure 2a shows the learning curves for all groups across all 3 days of the experiment. Day 1 learning of rotation A was very similar across groups and progressed through a gradual reduction in direction error from ~27° early on to ~8° by the end of the learning phase. We did not find any statistical differences in A learning across groups (Figure 2b). Our group (A-A, A-B-A, A-AB-A) x time (early, late) ANOVA revealed only a significant effect of time ($F_{(1,55)} = 881.72$, $p < 0.001$, $\omega^2 = 0.82$), but no significant effect of group ($F_{(2,55)} = 0.36$, $p = 0.697$, $\omega^2 = 0$) or group x time interaction ($F_{(2,55)} = 0.27$, $p = 0.763$, $\omega^2 = 0$). 24 hours after the initial learning of A, participants in the A-AB-A group actively practiced A again for a brief period of 24 trials (3 cycles). Direction errors were much lower (Figure 2c) from the outset of this reactivation period (14.269±1.136°) compared to early naïve A learning on day 1 (27.324±0.705°). This indicated that prior A learning was retained and could be quickly retrieved. Notably, by the end of reactivation, direction errors were already down to levels seen at the end of A learning on day 1. This pattern of results was supported by a significant day (day 1, day 2) x time (early, late) interaction ($F_{(1,18)} = 38.434$, $p < 0.001$, $\omega^2 = 0.363$), with post-hoc tests showing smaller direction errors at the early stage ($t_{(18)} = 9.632$, $p < 0.001$, CI for mean difference = [9.039, 17.069]) but not at the end ($t_{(18)} = 1.210$, $p = 0.242$, CI for mean difference = [-2.089, 4.976]) of naïve learning (day 1) and reactivation (day 2) periods.

Following reactivation, participants in the A-AB-A group were exposed to the opposing rotation B. Participants in the A-B-A group also experienced B on day 2, but without any reactivation of prior A learning. The A-AB-A group showed after-effects of practicing A on day 2 such that their direction errors during the early B learning phase (Figure 2d) were larger (-46.766±1.501°) than those in the A-B-A group (-40.854±1.085°). Errors gradually reduced in both groups, and no

differences were evident at the end of learning (Figure 2d). These results were supported by a significant group (A-B-A, A-AB-A) x time (early, late) interaction ($F_{(1,36)} = 5.057$, $p = 0.031$, $\omega^2 = 0.050$), with post-hoc tests showing significant differences in direction errors during early learning ($t_{(36)} = -3.192$, $p = 0.006$, CI for mean difference = [-11.083, -0.742]), but not at the end ($t_{(36)} = 0.250$, $p = 0.804$, CI for mean difference = [-5.767, 6.903]).

We then turned to our main question of whether performance upon re-exposure to A on day 3 would be worse for the reactivation group, as predicted by the reconsolidation theory. We compared the pattern of A learning on day 3 across our groups, and found a significant group (A-A, A-B-A, A-AB-A) x time (early, late) interaction ($F_{(2,55)} = 13.149$, $p < 0.001$, $\omega^2 = 0.085$). Post-hoc tests indicated significantly smaller direction errors for the A-A group relative to the A-B-A group ($t_{(55)} = -5.987$, $p < 0.001$, CI for mean difference = [-21.138, -6.812]) as well as the A-AB-A group ($t_{(55)} = -4.433$, $p < 0.001$, CI for mean difference = [-17.510, -3.184]) during the early learning phase (Figure 2e). Most critically, we found no significant difference between the A-AB-A and A-B-A groups ($t_{(55)} = -1.535$, $p = 0.302$, CI for mean difference = [-10.883, 3.626]) at this time point. Likewise, there was no significant difference in direction error between these two groups at the end of learning either ($t_{(55)} = -1.670$, $p = 0.302$, CI for mean difference = [-7.501, 2.214], Figure 2e). In sum, reactivation of A in the A-AB-A group did not lead to re-learning performance on day 3 that was any worse than the no-reactivation A-B-A group.

We also examined if there were any within group differences in A learning across days 1 and 3. A group (A-A, A-B-A, A-AB-A) x day (day 1, day 3) ANOVA on the direction errors across all trials of A learning, revealed a significant interaction effect ($F_{(2,55)} = 18.609$, $p < 0.001$, $\omega^2 = 0.092$). Post-hoc tests confirmed that errors were significantly lower in the A-A group on day 3 than day 1 ($t_{(55)} = 6.717$, $p < 0.001$, CI for mean difference = [3.164, 8.487]). Importantly though, this was not the case for either the A-B-A group ($t_{(55)} = -1.692$, $p = 0.963$, CI for mean difference = [-4.236, 1.225]) or the A-AB-A group ($t_{(55)} = 0.640$, $p = 1.000$, CI for mean difference = [-2.161, 3.300]). This indicated that these latter two groups, which adapted to the interfering rotation B did not show any differences in the pattern of the naïve learning of A on day 1 and its relearning on day 3. In sum, performance was not any worse during relearning for either of these groups.

The surprising absence of a larger impairment in A learning on day 3 in the A-AB-A group was at odds with predictions of the reconsolidation theory. We therefore turned to an alternate body of work that has suggested that reactivation might actually strengthen an existing memory

against interference, and thus aid - rather than impair - subsequent recall of prior learning (Herszage & Censor, 2017; Schlichting & Preston, 2014; Schrift et al., 2022). If this were the case, participants in the A-AB-A group (who underwent reactivation) should have shown smaller direction errors on day 3 despite experiencing the interfering rotation B. However, this did not occur. We wondered if this was because the learning of B was masking any reactivation mediated benefit from being uncovered during the testing of A on day 3. If so, these potential anterograde effects of B would then need to be removed prior to A learning on day 3.

To address this, in a second experiment, we recruited two new groups of participants and again divided them into two groups; in the A-AB-NA (n = 18) participants briefly reactivated A on day 2, subsequently underwent B learning, and then practiced null trials to wash it out prior to A learning on day 3. Participants of the A-B-NA (n = 19) learned B on day 2 without any reactivation of A, and this was also washed out prior to A learning on day 3. Any potential advantage of reactivation would be evident as smaller direction errors during relearning of A on day 3 for the A-AB-NA participants compared to the A-B-NA group.

Reactivation provided no benefit if the competing learning was washed out after 24 hours

Figure 3a shows the learning curves for the two groups across the 3 days of the experiment. As in experiment 1, learning of A on day 1 across both groups was canonical and progressed as a gradual reduction in direction error. Aside from a main effect of time ($F_{(1,35)} = 793.000$, $p < 0.001$, $\omega^2 = 0.862$), we did not find any group differences ($F_{(1,35)} = 0.438$, $p = 0.512$, $\omega^2 = 0$) or interaction ($F_{(1,35)} = 2.312$, $p = 0.137$, $\omega^2 = 0.010$) in a group (A-B-NA, A-AB-NA) x time (early, late) ANOVA (Figure 3b). When re-exposed to A on day 2, direction errors in the A-AB-NA group, were significantly lower than naive A learning (Figure 3c), indicating that the previously acquired A memory had been retained and was being retrieved. This was supported by a day (day 1, day 2) x time (early, late) interaction ($F_{(1,17)} = 84.297$, $p < 0.001$, $\omega^2 = 0.411$), with post-hoc tests showing smaller direction errors during early learning ($t_{(17)} = 10.240$, $p < 0.001$, CI for mean difference =[8.494, 15.481]), but not later ($t_{(17)} = 0.058$, $p = 0.954$, CI for mean difference = [-1.668, 1.734]) when the naïve (day 1) and reactivation (day 2) periods were compared.

When exposed to B, both groups showed errors in the opposite direction with larger direction errors in the A-AB-NA group due to after-effects of reactivating A (Figure 3d). We obtained a significant group (A-B-NA, A-AB-NA) x time (early, late) interaction ($F_{(1,35)} = 4.955$, $p = 0.033$, $\omega^2 = 0.046$), with post-hoc tests showing smaller direction errors in the A-B-NA compared to the A-

AB-NA group during early B learning ($t_{(35)}$ = -3.081, p = 0.008, CI for mean difference = [-17.825, -0.837]), but not at the end ($t_{(35)}$ = -1.072, p = 0.291, CI for mean difference = [-6.898, 3.075]). 24 hours after adapting to rotation B, the learning was washed out via null trials. These trials were like the familiarization trials, and were introduced to remove any potential anterograde effects that B learning might produce on the subsequent (re)learning of A. We found neither a group difference ($F_{(1,35)}$ = 0.696, p = 0.410, ω^2 = 0), nor a group x time interaction ($F_{(1,35)}$ = 2.643, p = 0.113, ω^2 = 0.015) in washout performance; only a significant time effect ($F_{(1,35)}$ = 8.064, p = 0.007, ω^2 = 0.060) was observed. This suggested that there was no difference in the washout pattern across groups (Figure 2e).

After washout, participants in both groups readapted to rotation A. We expected that if reactivation had protected the memory of A, it would be evident in the form of smaller errors on day 3 in the A-AB-NA group compared to the A-B-NA group. However, we found neither a significant main effect of group ($F_{(1,35)}$ = 0.003, p = 0.955, ω^2 = 0), nor a significant interaction ($F_{(1,35)}$ = 0.007, p = 0.933, ω^2 = 0) in a group x time ANOVA (Figure 3f). A significant, but uninteresting effect of time was present ($F_{(1,35)}$ = 203.669, p < 0.001, ω^2 = 0.617). We also examined potential within group differences in A learning across days 1 and 3. Our group (A-B-NA, A-AB-NA) x day (day 1, day 3) ANOVA, with data collapsed across all trials of A learning on days 1 and 3, revealed no significant effect of group ($F_{(1,35)}$ = 0.317, p = 0.577, ω^2 = 0), day ($F_{(1,35)}$ = 3.308, p = 0.078, ω^2 = 0.006) or group x day interaction ($F_{(1,35)}$ = 0.052, p = 0.821, ω^2 = 0). This suggested that relearning on day 3 in both groups was no different from their own learning of A on day 1. Collectively, these results suggested that reactivation did not appear to provide any benefit to the A-AB-NA participants compared to the no-reactivation A-B-NA group.

A reactivation-mediated benefit emerged when the competing learning was washed out immediately, preventing its consolidation

In experiment 2, we waited 24 hours after B was learned to wash out its effects. We deliberated whether this might be too late, and whether the washout must occur sooner if potential benefits of active retrieval of A are to be uncovered. Therefore, in experiment 3, we washed out B right after it had been learned on day 2 in both our groups: A-ABN-A (with reactivation, n = 18) and A-BN-A (no reactivation, n = 18). As in experiment 2, our main question was whether participants in the A-ABN-A group would demonstrate smaller errors compared to the A-BN-A group when relearning A on day 3, reflecting a reactivation-mediated benefit.

Figure 4a shows the learning curves for the two groups across the 3 days of the experiment. As observed in our first two experiments, adaptation to A on day 1 was customary; direction errors reduced from about 27° early on to about 9° by the end of the learning. There was a clear effect of time ($F_{(1,34)} = 580.318$, $p < 0.001$, $\omega^2 = 0.832$), but no group effect ($F_{(1,34)} = 3.365$, $p = 0.075$, $\omega^2 = 0.033$) or interaction ($F_{(1,34)} = 0.378$, $p = 0.543$, $\omega^2 = 0$) in a group (A-BN-A, A-ABN-A) x time (early, late) ANOVA for A learning on day 1 (Figure 4b). Thus, naïve A learning was not different between the groups. When exposed to A on day 2, direction errors in the A-ABN-A group, were significantly lower than naïve A learning, as expected. This was supported by a significant day (day 1, day 2) x time (early, late) interaction ($F_{(1,17)} = 175.535$, $p < 0.001$, $\omega^2 = 0.346$), with post-hoc tests indicating smaller direction errors early on ($t_{(17)} = 15.888$, $p < 0.001$, CI for mean difference = [9.169, 13.409]) but not later ($t_{(17)} = -0.507$, $p = 0.619$, CI for mean difference = [-1.934, 1.372]) during the naïve learning (day 1) and reactivation (day 2) periods (Figure 4c).

When exposed to B, both groups showed errors in the opposite direction, which were gradually reduced over trials. Although early direction errors in the A-ABN-A group (-42.049±1.669°) were greater than those in the A-BN-A group (-37.106±1.237°) reflecting the after-effects of reactivating A (Figure 4d), there was no statistically significant effect of group ($F_{(1,34)} = 1.489$, $p = 0.231$, $\omega^2 = 0.007$) or group x time interaction ($F_{(1,34)} = 3.970$, $p = 0.054$, $\omega^2 = 0.025$). There was only a main effect of time ($F_{(1,34)} = 310.654$, $p < 0.001$, $\omega^2 = 0.728$). This again indicated that participants in both groups adapted to B in a similar manner. The B learning was then immediately washed out through null trials. The idea, as in experiment 2, was to remove any potential anterograde effects that B learning might produce on the subsequent (re)learning of A the next day. We observed a significant effect of group ($F_{(1,34)} = 10.825$, $p = 0.002$, $\omega^2 = 0.123$) and also time ($F_{(1,34)} = 108.068$, $p < 0.001$, $\omega^2 = 0.485$), but the group x time interaction was not significant ($F_{(1,34)} = 0.574$, $p = 0.454$, $\omega^2 = 0$). On average, direction errors in the A-BN-A group were greater by 3.672±1.116°, and this small difference was present at the beginning and at the end of the washout block. Critically, the two groups did not differ in terms of the magnitude of change in hand deviation that occurred over the washout block (from early to late) ($t_{(34)} = -0.757$, $p = 0.454$, CI for mean difference = [-4.157, 1.9]).

Finally, participants in both groups readapted to rotation A on day 3 of the experiment. It is here that we saw meaningful differences. Firstly, we obtained significant group ($F_{(1,34)} = 5.553$, $p = 0.024$, $\omega^2 = 0.061$) as well as interaction ($F_{(1,34)} = 6.452$, $p = 0.016$, $\omega^2 = 0.038$) effects in a group (A-BN-A, A-ABN-A) x time (early, late) ANOVA performed on the hand deviation of A relearning. This suggested differences between the groups in terms of how their errors were reduced when re-exposed to A on day 3. Note also that the interaction term contains a number of comparisons that are unrelated to our hypothesis, which could dilute the strength of the overall effect. Just as an example, this analysis ends up comparing early learning in the A-ABN-A group to the late learning of the A-BN-A group, which is not a comparison of relevance. Nevertheless, post-hoc tests showed that there were no group differences between the groups at the early learning phase ($t_{(34)} = -0.752$, $p = 0.457$, CI for mean difference = [-6.423, 3.704], Figure 4f); however, errors were much lower for the A-ABN-A group during the late phase ($t_{(34)} = -3.317$, $p = 0.004$, CI for mean difference = [-11.050, -0.932], Figure 4f). We also probed within group differences in A learning across days 1 and 3. Our group (A-BN-A, A-ABN-A) x day (day 1, day 3) analysis, which compared overall A learning between the two group across the two days, revealed a significant group effect ($F_{(1,34)} = 5.115$, $p = 0.030$, $\omega^2 = 0.056$) and a (marginal) interaction ($F_{(1,34)} = 4.258$, $p = 0.047$, $\omega^2 = 0.013$). We followed this up with separate day-wise comparisons for each group and noted that while direction errors of A learning were not different between days 1 and 3 in the A-BN-A group ($t_{(17)} = -0.962$, $p = 0.349$, CI for mean difference = [-3.115, 1.164]), they were significantly lower on day 3 than day 1 for the A-ABN-A group ($t_{(17)} = 2.558$, $p = 0.02$, CI for mean difference = [0.246, 2.562]). Thus, the results of multiple analyses converged to indicate that errors during relearning A on day 3 were smaller in the group that reactivated A on day 2 compared to the group that did not.

As a final check, we asked whether the benefit of reactivation that we observed in our third experiment was because reactivation itself was somehow different across the groups that received it. We performed a group (A-AB-A, A-AB-NA, A-ABN-A) x time (early, late) analysis on the direction errors of the reactivation session of day 2. We found neither a significant group effect ($F_{(2,52)} = 0.296$, $p = 0.745$, $\omega^2 = 0$) nor a significant interaction ($F_{(2,52)} = 0.118$, $p = 0.889$, $\omega^2 = 0$). Only a significant effect of time ($F_{(2,52)} = 215.684$, $p < 0.001$, $\omega^2 = 0.4$) was evident, indicating that there was no difference in performance across the groups that underwent reactivation of A on day 2 (Figure 5). This ruled out the possibility that the advantage seen in experiment 3 was somehow related to some difference in the way reactivation proceeded across the groups.

DISCUSSION

In this study, our main goal was to investigate the fate of a consolidated motor memory when it is reactivated and subsequently challenged with a competing one within an error-based motor learning framework. To do so, we employed different variants of the classic 3-day A-B-A paradigm in three different experiments. We first found, in line with past work (Caithness, 2004; Krakauer, 2009; Krakauer et al., 2005), that acquiring two competing motor memories (A and B) in succession results in significant interference between them. Specifically, when participants were retested on A after learning B, there was no detectable retention of the original memory. Second, this effect was independent of reactivation, indicating that reactivation was not necessary for the original memory to be disrupted by a competing one. Third, and most intriguingly, we found that reactivation could, under certain conditions, protect a memory against degradation by competing ones. This facilitatory effect was uncovered when the competing memory B was washed out right after its acquisition, effectively preventing its consolidation.

Our first set of results that interference is independent of reactivation is at odds with predictions of reconsolidation theory. According to this framework, it is active retrieval that makes a previously consolidated memory temporarily labile and susceptible to modification from a competing source (Gabitov et al., 2017, 2019; Lee et al., 2017; Schiller & Phelps, 2011; Trent et al., 2015; Walker et al., 2003). This is manifested as worse performance when the original memory is reassessed. Our results deviate from this expectation in two major ways. Firstly, we found no evidence that reactivation exacerbated the interference effect. Specifically, the group that underwent reactivation did not exhibit worse performance on retest compared to the group that did not reactivate. These findings align with some notable past studies that failed to replicate reconsolidation effects in motor sequence learning (Censor et al., 2016; de Beukelaar et al., 2014; Hardwicke et al., 2016), and suggest that reactivation does not necessarily amplify the vulnerability of a motor memory to competing inputs. Secondly, we observed that reactivation was not even necessary for the original memory (of A) to be modified (by B), indicating that memory modification in error-based motor learning can occur without the original memory being destabilized through active retrieval.

A plausible explanation for these findings may be that rather than labile and consolidated states, motor memories transition between active and inactive states (Caithness, 2004; Censor et al.,

2010; Lewis, 1979). Thus, when a memory is first forged (during adaptation to A in our case), it transitions from an initial active state where it is readily accessible and modifiable to an inactive state where it is stored but not immediately accessible. When a participant re-engages with the task, regardless of the specific trial features (re-exposure to A, or exposure to B), the original memory (of A) returns to the active state and becomes susceptible to change. Thus, the overall task context, i.e. performing the same reaching task in the same set up, may be a sufficient cue in getting a past memory back online without the need for its explicit retrieval or rehearsal. This also aligns with broader theories of memory that emphasize the role of context in memory retrieval and modification, evident in domains such as episodic, fear and motor sequence memories (Gershman et al., 2013; Heald et al., 2021; Hupbach et al., 2007; Nadel & Sederberg, 2024). The fate of the previous memory (of A) once it is brought to an active state through contextual priming might then depend critically on the specific task and trial structure that follows. If participants practice the competing task B, the original memory of A is likely to be significantly altered by it. In contrast, if participants practice task A, even if briefly, the additional exposure may serve to strengthen the already active memory of A, reinforcing its stability and resistance to interference. This raises the intriguing possibility that what is traditionally considered “reactivation” in such paradigms might in fact function as additional training on A. It is well-established that overtraining a motor skill strengthens the associated memory, making it more resistant to interference (Krakauer et al., 2005; Shadmehr & Brashers-Krug, 1997). We speculate that a similar mechanism may have been at work in our study. When participants performed trials involving adaptation to A on day 2, even if these trials were intended solely to reactivate the memory, they may have inadvertently provided additional practice, thereby strengthening the memory of A against interference from the B learning that followed.

We must point out though that the protection of A following reactivation was only evident when we used null trials to wash out the competing memory B immediately after it was learned (experiment 3, A-ABN-A group). In contrast, when B was washed out 24 hours after it was learned in experiment 2 (A-AB-NA group), protective benefits were not observed. A parsimonious explanation for this difference may be that the memory was likely strengthened against interference in both experiments (and even in experiment 1 in the A-AB-A group), because the reactivation process itself was identical. However, the 24-hour gap between subsequent B learning and washout in experiment 2 (and re-test of A in experiment 1) allowed the memory of B to consolidate, and override, in a retrograde manner, any benefits conferred by the active rehearsal of A. As a result, performance became similar to the no-reactivation groups

of these experiments (A-B-A group in experiment 1, A-B-NA group in experiment 2). However, in experiment 3, because B was washed out immediately after learning, retrograde effects were minimized, and reactivation-mediated gains were likely preserved and reconsolidated, ultimately manifesting as smaller directional errors upon re-exposure to A on day 3 compared to the no-reactivation group.

Another possibility underlying the differential effects of reactivation across our experiments relates to the anterograde rather than retrograde effects of learning B. Specifically, in experiments 1 and 2, B learning may have blocked the recall of the protected memory of A on day 3, thereby masking any reactivation-mediated benefit. This was likely prevented in experiment 3 due to the immediate washout of B and an attenuation of its anterograde effects. Moreover, while there was no washout in experiment 1, the washout trials implemented 24 hours after learning B in experiment 2 may have been ineffective in eliminating any potential anterograde effects since B had already consolidated by that time. Indeed, close inspection of the behavior on the washout trials in experiment 2 revealed that participants did not exhibit any after-effects of B learning on day 3, with direction errors on the day 3 null trials being close to zero (figure 3). In essence, once was B was consolidated, there was little left to “wash out” and performance effectively mirrored that of the A-AB-A group of experiment 1. Future studies, such as those that specifically manipulate the timing between the learning of B and testing of A, could disambiguate the retrograde versus anterograde causes of the absence of reactivation-mediated benefits in paradigms such as those used in experiments 1 and 2.

It may also perhaps be worthwhile to discuss what the differences between the reactivation and no-reactivation groups in experiment 3 are unlikely to be a consequence of. Firstly, we do not think that the observed difference can be attributed to simple contextual dissimilarity effects. As emphasized earlier, “context” in our paradigm likely encompasses broader elements such as the task apparatus, the laboratory environment, and the general nature of the reaching movements, rather than the specific perturbations (A or B) that participants in the reactivation and no-reactivation groups experience on day 2. Thus, there was likely substantial contextual overlap rather than dissimilarity between the two groups, making it unlikely that contextual dissimilarity determines the reactivation-mediated benefits seen in experiment 3. Moreover, if contextual dissimilarity were playing a role, we would have expected to see a similar effect in experiment 2, where the initial trials on day 2 were identical to those in experiment 3. The only difference between the two experiments was the timing of the washout procedure – immediate in

experiment 3 versus delayed by 24 hours in experiment 2. The absence of reactivation-mediated benefits in experiment 2, despite the identical initial conditions, weakens the argument that contextual variability is a determinant of the effect. Instead, the critical difference appears to lie in whether the competing memory (B) was allowed to consolidate before being washed out or not.

Secondly, it is also unlikely that the protection of A observed in experiment 3 is merely due to group differences in the washout pattern on null trials introduced post B learning. Note that the difference in direction error between the reactivation (A-ABN-A) and the no-reactivation (A-BN-A) groups was about ~3°, with the reactivation group showing smaller errors. Thus, if unequal washout had left more of B memory “alive” in the A-BN-A group, this difference should have been apparent during the early relearning of A on day 3 as well. This was not the case; both groups started at comparable error levels (A-BN-A: 25.332±1.604° and A-ABN-A: 23.972±0.833°), and by the end of relearning, differed by ~6°. Thus, it was not some kind of offset that was simply being carried over from washout to relearning. Rather the evolution of the smaller errors in the reactivation group over the course of the relearning period pointed to an advantage that this group had that the no-reactivation group did not. We suggest that this advantage came from active retrieval and practice of A during the reactivation period.

One could argue that the ~6° benefit provided by reactivation was modest in absolute terms. This could simply be due to the limited number of reactivation trials (only 3 cycles) used in our paradigm. It is not unreasonable to expect that a greater number of reactivation trials would yield a more substantial benefit (de Beukelaar et al., 2014, 2016; Forcato et al., 2013); this could also be investigated in subsequent work. Another interesting question that could be examined going forward is whether a greater number of reactivation trials would also afford protection against interference when the competing memory (B) is allowed to consolidate, as in our experiments 1 and 2.

It is not uncommon in reconsolidation studies across various memory domains to draw a hard distinction between reactivation-mediated protection of a prior memory or its weakening. This is the case because the experimental paradigms that probe these two aspects are often fundamentally different. Rarely do the studies that argue in favor of protection or strengthening challenge the reactivated memory with a competing one, and seldom does a paradigm demonstrating weakening of an existing memory trace not use a competing input. Our results

caution against this binary framework; we show that strengthening can manifest as greater resistance to interference from a competing input. In other words, the protective effect of reactivation does not merely involve enhancing memory stability in isolation but may also involve shielding the memory from being disrupted by new, conflicting information. This suggests that the traditional distinction between strengthening and weakening may be overly simplistic. Instead, reactivation may serve a more nuanced role, simultaneously stabilizing memories and making them more resilient to interference.

Our results also pave the way for exploring several new questions about motor memory reconsolidation in the future. In animal studies, it is well-established that the weakening or strengthening of memories is governed by a set of “boundary conditions”. These include factors such as the age of the memory, the intensity of initial training, the duration of reactivation, the novelty of information introduced during reactivation, and the time elapsed between reactivation and the interfering intervention (de Beukelaar et al., 2014, 2016; Fernández et al., 2016; Mooney et al., 2021; Nadel & Sederberg, 2024; Ritvo et al., 2019; Sinclair & Barense, 2019). While these boundary conditions are less clearly defined in human studies (Auber et al., 2013; Schiller & Phelps, 2011), research in episodic memory has shown that reactivating general, rather than specific, details about a prior episode can make the memory more resistant to disruption by newer information (Koen & Rugg, 2016; Potts & Shanks, 2012; Schiller et al., 2010). Similarly, in the motor domain, increasing sensorimotor variability during reactivation has been shown to enhance the strength of the prior memory (Wymbs et al., 2016). The effects of such factors on the reactivation-mediated resistance to interference, as observed in our study, could be very interesting directions that future studies could pursue. Addressing these questions could provide deeper insights into the mechanisms underlying reconsolidation in motor learning and help identify optimal conditions for enhancing memory retention and resilience. Such findings could also inform the development of more effective skill learning and rehabilitation protocols, particularly in contexts where minimizing interference from multiple competing motor inputs is critical.

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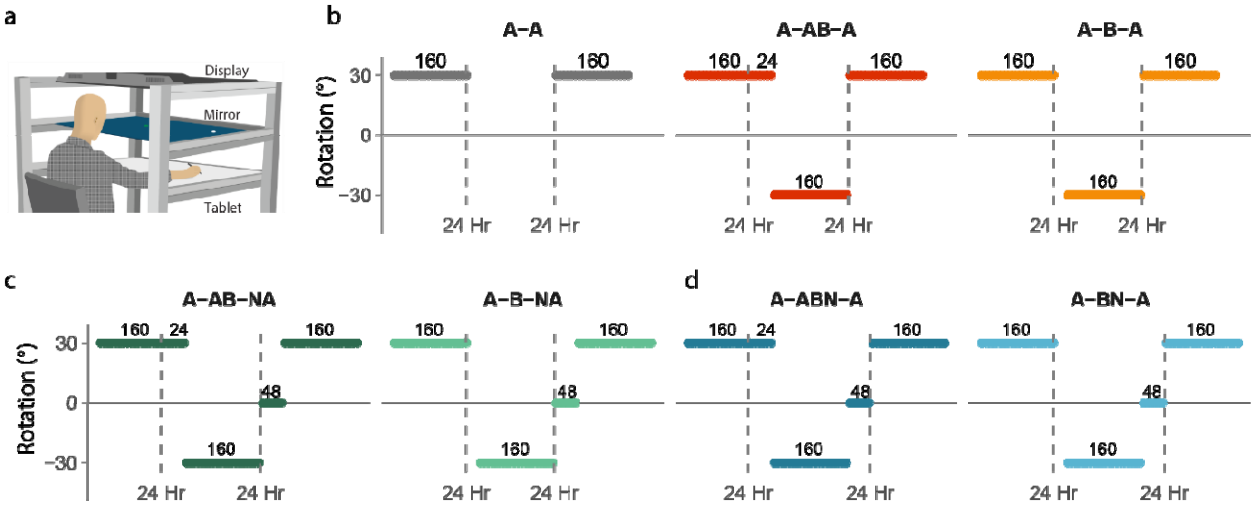

Figure 1. (a) Experimental setup comprising of a virtual reality system that restricted movements to the horizontal plane. Participants performed arm-reaching movements on a digitizing tablet while looking into a mirror placed between the tablet and a horizontally mounted high-definition display. Feedback about hand position was displayed via the display onto the mirror using a cursor. **(b-d)** Trial structure for the different groups of (b) experiment 1, (c) experiment 2 and (d) experiment 3. Across experiments participants performed variants of a 3-day A-B-A visuomotor adaptation task, wherein following baseline practice, they learned a 30° counterclockwise rotation A on day 1, followed by a competing 30° clockwise rotation B on day 2, and were retested on A on day 3, either with or without reactivation.

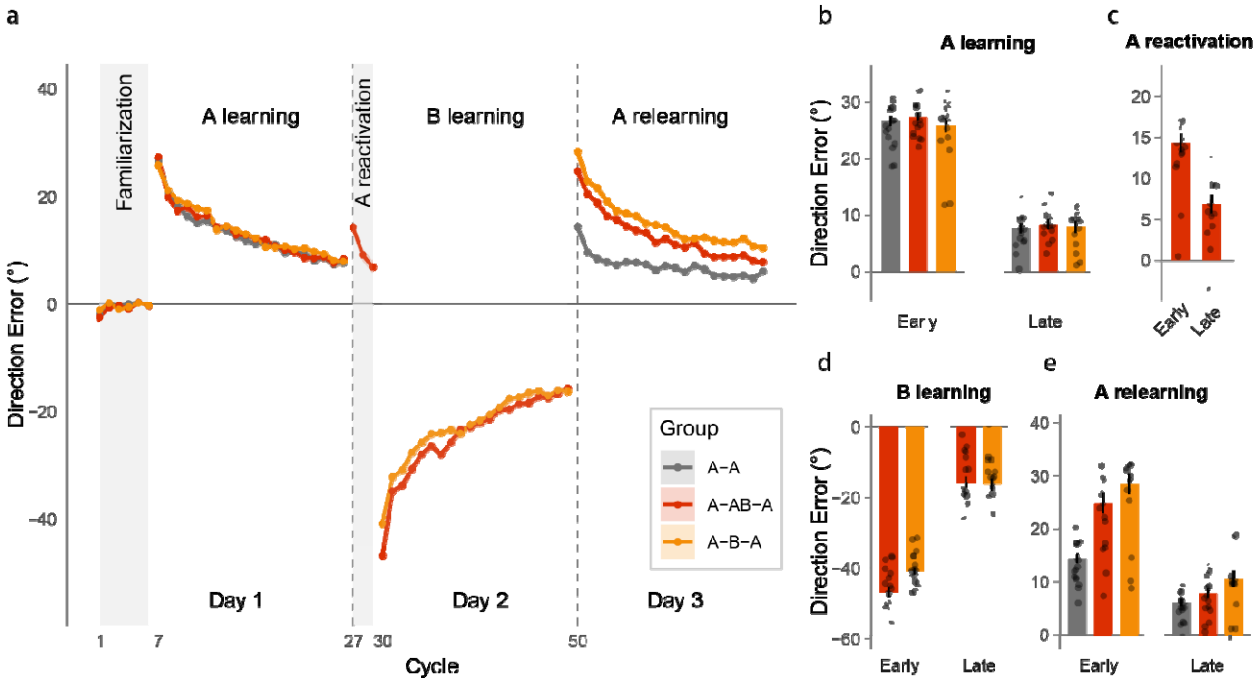

Figure 2. (a) Learning curves showing mean direction error as a function of cycles, plotted for the different blocks of experiment 1. The reactivation group (A-AB-A) is shown in red, the no-reactivation group (A-B-A) in orange, and the control group (A-A) in gray. Dark vertical dashed lines represent 24-hour intervals between the blocks. Shaded areas represent SEM. **(b, c, d, e)** Mean ± SEM direction error during early (first 8 trials) and late learning (last 8 trials) phases for each learning block. Dots represent individual participants.

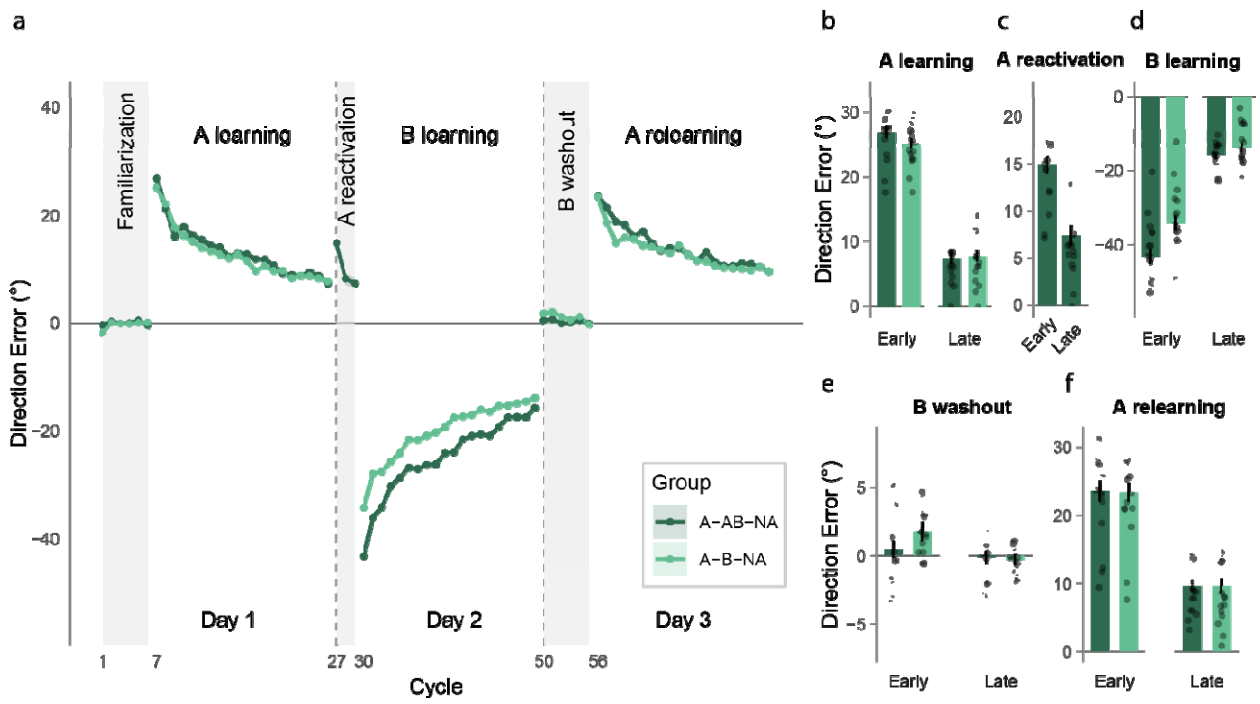

Figure 3. (a) Learning curves showing mean direction error as a function of cycles, plotted for the different blocks of experiment 2. The reactivation group (A-AB-NA) is shown in dark green, while the no-reactivation group (A-B-NA) is in light green. Dark vertical dashed lines represent 24-hour intervals between the blocks. Shaded areas represent SEM. **(b, c, d, e, f)** Mean ± SEM direction error during early and late phases of the different learning and washout blocks. Dots represent individual participants.

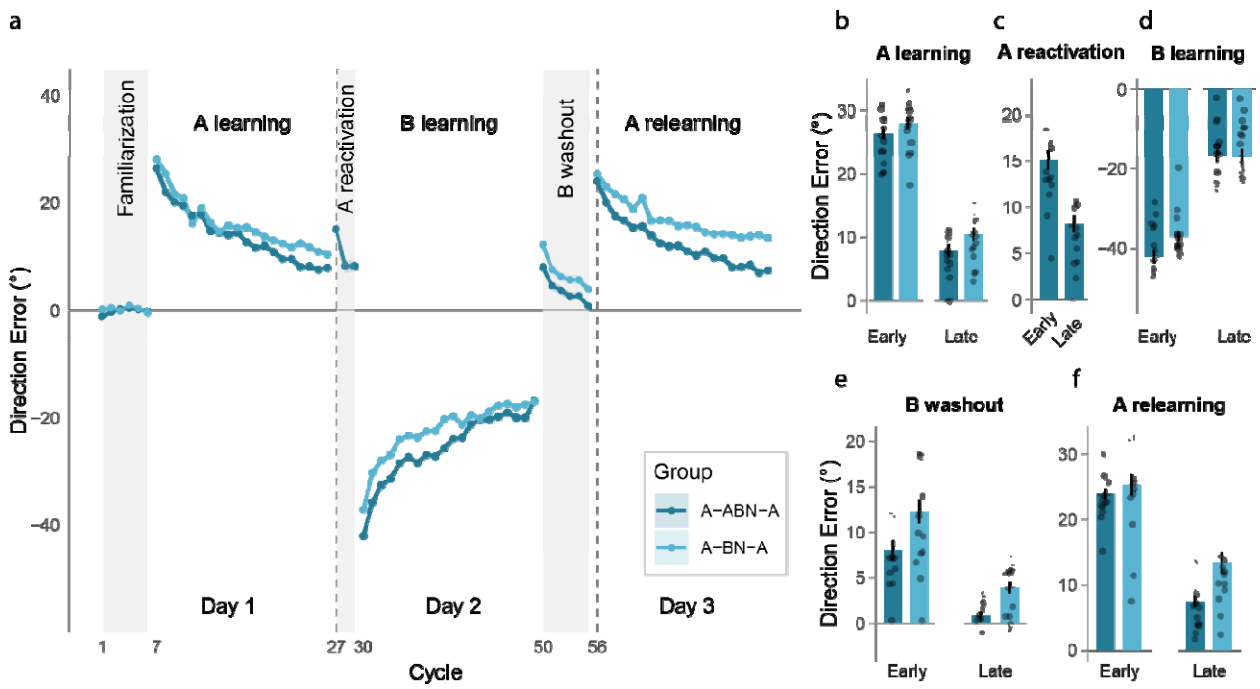

Figure 4. (a) Learning curves showing mean direction error as a function of cycles, plotted for the different blocks of experiment 3. The reactivation group (A-ABN-A) is shown in dark blue, while the no-reactivation group (A-BN-A) is in light blue. Dark vertical dashed lines represent 24-hour intervals between the blocks. Shaded areas represent SEM. **(b, c, d, e, f)** Mean ± SEM direction error during early and late phases of the different learning and washout blocks. Dots represent individual participants.

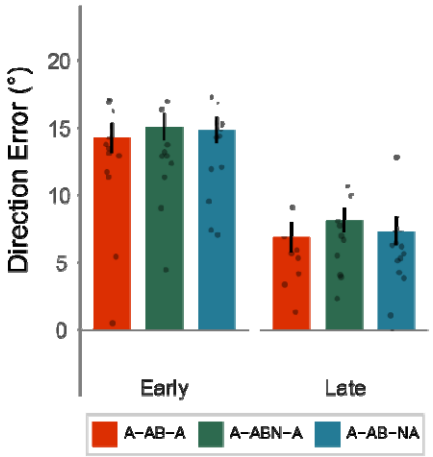

Figure 5. Mean ± SEM direction error during the early and late phases of the reactivation block for the three reactivation groups: A-AB-A (red), A-AB-NA (green) and A-ABN-A (blue). Dots represent individual participants.