

Differential development of retroactive and proactive interference during post-learning wakefulness

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Newly encoded, labile memories are prone to disruption during post-learning wakefulness. Here we examine the contributions of retroactive and proactive interference to daytime forgetting on an auditory classification task in a songbird. While both types of interference impair performance, they do not develop concurrently. The retroactive interference of task-B on task-A developed during the learning of task-B, whereas the proactive interference of task-A on task-B emerged during subsequent waking retention. These different time courses indicate an asymmetry in the emergence of retroactive and proactive interference and suggest a mechanistic framework for how different types of interference between new memories develop.

[Supplemental material is available for this article.]

Learning initiates a process of memory consolidation that leads to the formation of stable, long-term memories (McGaugh 2000; Bailey et al. 2015; Squire et al. 2015). Before being stabilized, new memory traces reside in a labile state in which they are susceptible to disruption, such as interference from other learning, and subsequent forgetting (Wixted 2004). It is widely believed that sleep, particularly the first post-learning instance of sleep, is critical for consolidating labile memory traces into more stable forms (Paller and Voss 2004; Ribeiro and Nicolelis 2004; Rasch and Born 2013; Tononi and Cirelli 2014; Brawn and Margoliash 2015). This suggests that newly encoded memories are especially susceptible to disruption during the waking interval between initial learning and sleep.

Given that new information and skills can be acquired rapidly each day, examining how labile memories interact is crucial to understanding how memories are formed or forgotten (Wixted 2004, 2005). When two memory tasks are learned sequentially (i.e., task-A followed by task-B), two types of interference may develop. In retroactive interference, the learning of a new task (task-B) impairs the retention of the previously learned task (task-A). In proactive interference, the learning of task-A before task-B impairs the ability to learn or remember task-B.

We have previously shown that European starlings trained on two similar auditory classification tasks exhibit impaired performance on both tasks when tested at the end of the training day (Brawn et al. 2013). While this shows that two labile memories can negatively impact each other, it remains unknown when the interference developed because the memory for each task was only retested in the evening. Do retroactive and proactive interference develop in concert as the second task is being learned, do they develop together during the subsequent post-learning retention period, or does the interference between tasks develop asymmetrically? Likewise, do memories diminish without interfering experiences in a time-dependent manner?

Research on memory has not provided substantial support for a “pure decay” mechanism of forgetting (e.g., Galotti 2008; Ashcraft and Radvansky 2010; but see Berman et al. 2009; Frankland et al. 2013; Hardt et al. 2013, Sadeh et al. 2014, 2016), but single-task conditions establish a baseline for any changes that occur over time without interference. Here, in two experiments, we trained starlings on one or two classification tasks and retested the tasks at two later time points that day to examine how interference between new labile memories develops across wakefulness prior to the first night of sleep consolidation.

Thirty adult European starlings completed each of the four conditions from experiment-1 (Fig. 1A). Starlings were given free access to water but were only given food via correct performance on a Go/No-Go auditory classification task (Brawn et al. 2010, 2013). In this task, starlings initiated stimulus playback by probing a response port with their beak. After stimulus completion, starlings had 2-sec to probe a second response port or to withhold response. Responding to one stimulus (Go) produced a 4-sec food reward, while responding to the other stimulus (No-Go) resulted in a 15-sec lights-out punishment. Nothing occurred if the starlings did not respond. Each starling became familiar with the Go/No-Go procedure by learning a baseline classification task with the baseline stimulus pair during the weeks prior to starting the experiment. The baseline stimuli consisted of a rising tone sweep (1–2 KHz) or a falling tone sweep (3–2 KHz) repeated three times for a total duration of 1.7-sec. Starlings were also engaged in the baseline classification task on experimental days whenever they were not completing training/testing sessions on the experimental stimuli and on the days in between conditions. For the experimental conditions, the stimuli consisted of novel pairs of 5-sec segments of starling song. The two stimuli within a pair were recorded from a single bout of starling song, and each stimulus pair was recorded from a different starling. Stimulus pairs were assigned randomly for each bird in each condition. Each training

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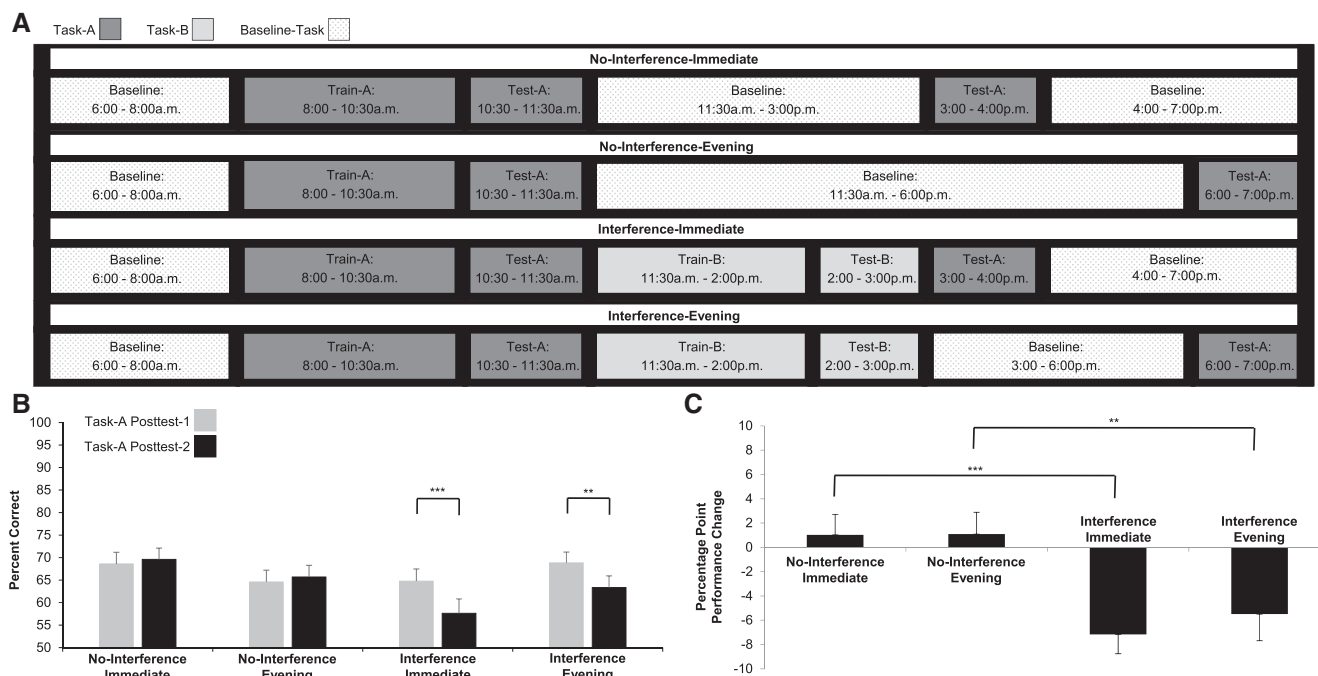


Figure 1. Experiment-1 design and results. Starlings were trained to classify song stimuli and tested two times during the day. (A) The conditions followed a Train/Test-A → Retest-A (two conditions without task-B interference) or a Train/Test-A → Train/Test-B → Retest-A (two conditions with task-B interference) design, with two nights of sleep separating each condition. Starlings in each condition were trained and tested on classification task-A in the morning from 8:00 a.m. to 11:30 a.m. In the two interference conditions, starlings were then immediately trained and tested on classification task-B from 11:30 a.m. to 3:00 p.m. The “No-Interference-Immediate” and “Interference-Immediate” conditions were retested on task-A at 3:15 p.m. This was the time point immediately after the task-B test session for the interference conditions (including the 15 min of free access to food that began each test session), which was 3.75 h after the task-A post-training test session. The “No-Interference-Evening” and “Interference-Evening” conditions were retested on task-A at 6:15 p.m. This occurred 3 h after the task-B test session for the interference conditions, which was 6.75 h after the task-A post-training test session. The order of conditions was counterbalanced across all starlings, and the stimulus pairs used in each condition were randomly assigned for each bird. (B) The mean percentage of trials responded to correctly in the post-training (post-test-1, gray bars) and post-retention (post-test-2, black bars) classification task-A tests is shown for each condition. (C) The mean percentage point change is shown for each condition. Asterisks denote significant differences between (B) performance at the two test points and (C) performance changes across conditions. (** $P < 0.01$; *** $P < 0.001$). Comparisons were analyzed using *t*-tests with Holm’s Bonferroni procedure to correct for multiple comparisons. Error bars show standard error of the mean.

session lasted 2.5-h during which starlings could complete up to 270 trials. The stimulus for each training trial was selected randomly, except that the same stimulus was selected for the next trial whenever a starling responded incorrectly, for up to three consecutive errors. Starlings received 15-min of free access to food at the start of each test session, which was followed by a 45-min period during which the starlings could complete up to 30 test trials. The reward contingencies during testing were identical to the training session, and the test stimuli were selected randomly but constrained such that each stimulus was selected five times for every 10 trials. Performance was measured as the percentage of correct trials during a test session, where a correct trial entailed responding to a Go stimulus or withholding response to a No-Go stimulus (see Supplemental Material for response rates to the Go and No-Go stimulus classes analyzed separately). Performance improvement scores were calculated by subtracting the percent correct score of the post-training test (post-test-1) from the post-retention test (post-test-2).

Classification accuracy averaged across the four conditions on the post-training classification task-A tests was $66.7 \pm 1.6\%$ (mean \pm SEM). This performance level was significantly greater than chance performance of 50% ($t_{(29)} = 10.49$, $P < 0.001$), confirming that a single training session produced significant auditory classification learning in the starlings (Brawn et al. 2010, 2013). Having learned task-A, starlings in the two interference conditions also learned the second classification task-B. Performance accuracy av-

eraged across the two interference conditions on the post-training classification task-B test was $70.7 \pm 2.1\%$, also significantly above chance ($t_{(29)} = 9.75$, $P < 0.001$). Post-training test performance on task-A immediately after the task-A training session did not differ across the conditions ($F_{(3,87)} = 0.99$, $P = 0.40$). Likewise, post-training test performance on task-B immediately after task-B training did not differ between the two interference conditions ($t_{(29)} = 0.56$, $P = 0.56$). However, for the interference conditions, performance on the post-training task-B test was marginally greater than performance on the preceding post-training task-A test ($t_{(29)} = 1.71$, $P < 0.10$).

To evaluate performance on classification task-A following training and retention, we conducted a 2 (Test: Post-Train; Post-Retention) \times 4 (Condition: Interference-Immediate; Interference-Evening; No-Interference-Immediate; No-Interference-Evening) repeated-measures ANOVA. Significant differences were obtained for the Test ($F_{(1,29)} = 6.85$, $P < 0.05$) and the Test \times Condition interaction ($F_{(3,87)} = 5.95$, $P = 0.001$). There was also a marginally significant effect for Condition ($F_{(3,87)} = 2.36$, $P < 0.10$). Task-A performance in the No-Interference conditions showed nonsignificant percentage point gains from the post-training to the post-retention test of 1.0 ± 1.7 for No-Interference-Immediate ($t_{(29)} = 0.60$, $P = 0.55$) and of 1.1 ± 1.8 for No-Interference-Evening ($t_{(29)} = 0.59$, $P = 0.56$). In contrast, task performance in the Interference conditions exhibited significant losses of 7.2 ± 1.6 for Interference-Immediate ($t_{(29)} = 4.47$, $P < 0.001$) and of 5.5 ± 2.2 for

Interference-Evening ($t_{(29)} = 2.54, P < 0.05$) (Fig. 1B). We thus tested specific comparisons to assess the effects of retroactive interference on classification performance across waking retention. There were no significant differences between the No-Interference-Immediate and No-Interference-Evening conditions ($t_{(87)} = 0.04, P = 0.97$) or between the Interference-Immediate and Interference-Evening conditions ($t_{(87)} = 0.94, P = 0.35$). However, there were significant differences between the Interference and No-Interference conditions at the Immediate retest ($t_{(87)} = 4.62, P < 0.001$) as well as between the Interference and No-Interference conditions at the Evening retest ($t_{(87)} = 3.70, P < 0.001$) (Fig. 1C). Finally, the overall performance loss in the immediate and evening interference conditions was mediated by impaired performance on the No-Go stimulus class. Indeed, an analysis of performance separated by stimulus class revealed nonsignificant gains of 2.1 ± 2.4 ($t_{(29)} = 0.86, P = 0.40$) and 3.8 ± 4.3 ($t_{(29)} = 0.88, P = 0.38$) to the Go stimuli but significant losses of 14.8 ± 4.0 ($t_{(29)} = 3.71, P < 0.001$) and 10.5 ± 4.8 ($t_{(29)} = 2.21, P < 0.05$) to the No-Go stimuli for the Interference-Immediate and Interference-Evening conditions, respectively (Supplemental Figs. S9, S10).

These results demonstrate that the memory for task-A did not deteriorate, after 3.75 or 6.75 h, when only one task was learned. Yet, the learning of task-B retroactively interfered with task-A performance. Importantly, the effect of task-B interference on task-A performance was evident immediately after task-B training and therefore developed while task-B was being learned. Since we know that the learning of task-A can also impair the memory for

task-B (Brawn et al. 2013), does the proactive interference of task-A on task-B also develop during task-B acquisition? Consequently, in experiment-2, we examined the development of the proactive interference of task-A on task-B. Thirty starlings completed each of the four conditions from experiment-2 (Fig. 2A). For reasons of animal availability, five of the starlings had also completed experiment-1. The same baseline stimulus set was used in both experiments, but the stimulus pairs for the experimental sessions in experiment-2 were different from experiment-1. The procedures, performance measures, and statistical analyses were identical to experiment-1.

Classification accuracy averaged across the four conditions on the post-training classification task-B tests was $78.5 \pm 2.2\%$. This performance level was significantly greater than chance performance of 50% ($t_{(29)} = 12.83, P < 0.001$). Likewise, starlings in the interference conditions also learned classification task-A prior to task-B training. Performance accuracy averaged across the two interference conditions on the post-training task-A test was $69.0 \pm 2.4\%$, which was also significantly above chance ($t_{(29)} = 7.8, P < 0.001$). Post-training test performance was found to differ across the conditions on task-B ($F_{(3,87)} = 3.52, P < 0.05$) but did not differ for the interference task-A test ($t_{(29)} = 0.17, P = 0.86$). Moreover, for the interference conditions, performance on the post-training task-B test was significantly greater than performance on the preceding post-training task-A test ($t_{(29)} = 4.83, P < 0.001$).

To evaluate performance on classification task-B following training and retention, we conducted a 2 (Test: Post-Train,

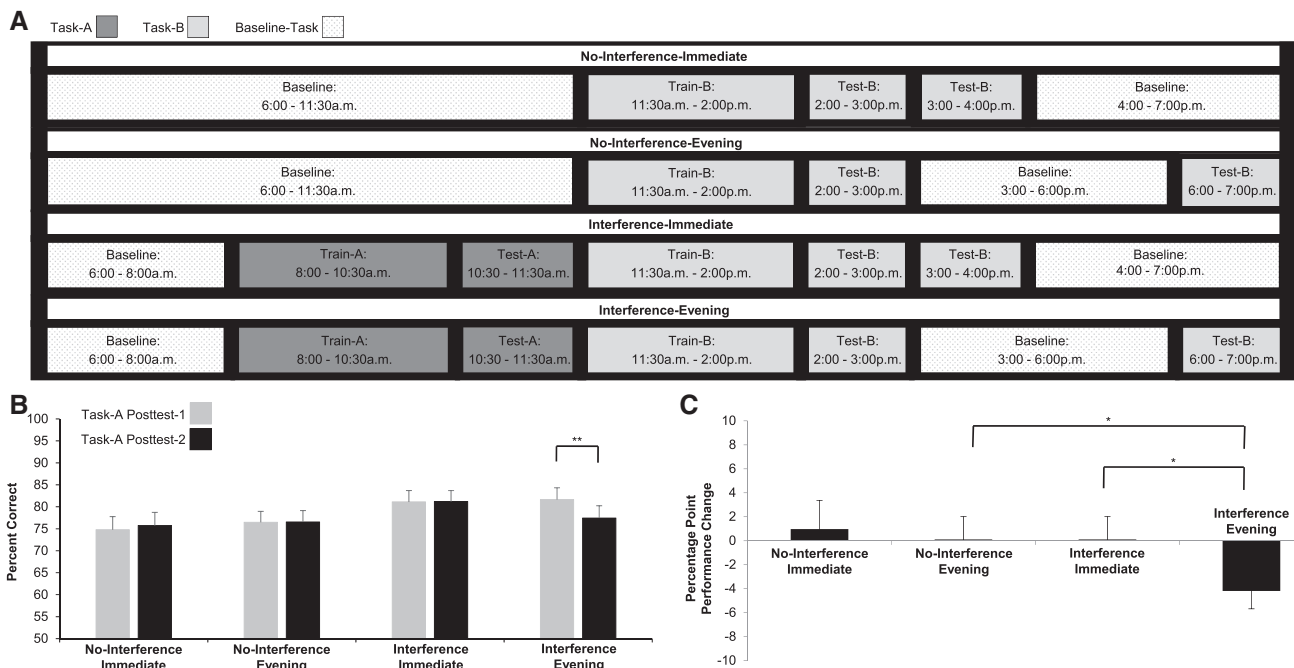


Figure 2. Experiment-2 design and results. Starlings were trained to classify song stimuli and tested two times during the day. (A) The conditions followed a Train/Test-B \rightarrow Retest-B (two conditions without task-A interference) or a Train/Test-A \rightarrow Train/Test-B \rightarrow Retest-B (two conditions with task-A interference before learning task-B) design, with two nights of sleep separating each condition. Each condition provided training and testing on classification task-B from 11:30 a.m. to 3:00 p.m. The two interference conditions provided additional training and testing on classification task-A immediately prior to task-B training from 8:00 a.m. to 11:30 a.m. The “No-Interference-Immediate” and “Interference-Immediate” conditions were retested on task-B at 3:15 p.m., which was the time point immediately after the task-B post-training test session (after 15 min of free access to food). The “No-Interference-Evening” and “Interference-Evening” conditions were retested on task-B at 6:15 p.m. This occurred 3 h after the task-B post-training test session, which was 6.75 h after the task-A post-training test session for the interference condition. The order of conditions was counterbalanced across all starlings, and the stimulus pairs used in each condition were randomly assigned for each bird. (B) The mean percentage of trials responded to correctly in the post-training (post-test-1, gray bars) and post-retention (post-test-2, black bars) classification task-B tests is shown for each condition. (C) The mean percentage point change is shown for each condition. Asterisks denote significant differences between (B) results at the two tests points and (C) performance changes across conditions. (* $P < 0.05$; ** $P < 0.01$). Comparisons were analyzed using t -tests with Holm’s Bonferroni procedure to correct for multiple comparisons. Error bars show standard error of the mean.

Post-Retention) \times 4 (Condition: Interference-Immediate; Interference-Evening; No-Interference-Immediate; No-Interference-Evening) repeated-measures ANOVA. While there was not a significant effect for Test ($F_{(1,29)} = 0.66, P = 0.42$), there were marginally significant effects for Condition ($F_{(3,87)} = 2.61, P < 0.10$) and the Test \times Condition interaction ($F_{(3,87)} = 2.15, P = 0.10$). Task-B classification performance showed nonsignificant percentage point gains from the post-training to the post-retention tests of 1.0 ± 2.1 for the No-Interference-Immediate condition ($t_{(29)} = 0.47, P = 0.64$), of 0.1 ± 1.6 for the No-Interference-Evening condition ($t_{(29)} = 0.05, P = 0.96$), and of 0.1 ± 1.6 for the Interference-Immediate condition ($t_{(29)} = 0.05, P = 0.96$). By comparison, the Interference-Evening condition exhibited a significant performance loss of 4.2 ± 1.3 ($t_{(29)} = 3.21, P < 0.01$) (Fig. 2B). We further tested specific comparisons to assess the effects of proactive interference on classification performance across waking retention. There were no significant differences between the No-Interference-Immediate and No-Interference-Evening conditions ($t_{(87)} = 0.56, P = 0.58$) or between the No-Interference and Interference conditions at the Immediate retest ($t_{(87)} = 0.55, P = 0.60$). However, performance in the Interference-Evening condition was significantly lower than the Interference-Immediate condition ($t_{(87)} = 2.70, P < 0.05$) and the No-Interference-Evening condition ($t_{(87)} = 2.69, P < 0.05$) (Fig. 2C). In contrast to the case of retroactive interference in experiment-1, the overall performance loss in the Interference-Evening condition did not exclusively result from impaired performance on the No-Go stimulus class but rather from the combined nonsignificant performance decrement of 3.8 ± 2.4 to the Go stimuli ($t_{(29)} = 1.57, P = 0.13$) and the marginally significant decrement of 4.6 ± 2.4 to the No-Go stimuli ($t_{(29)} = 1.86, P < 0.10$) (Supplemental Figs. S11, S12). The different response patterns to the Go and No-Go stimulus classes for the cases of retroactive and proactive interference may suggest an asymmetry in how retroactive and proactive interference are behaviorally expressed.

The results from experiment-2 demonstrate that the memory for task-B remained stable across 3.25 h of waking retention when only task-B was learned. However, the learning of task-A prior to task-B proactively interfered with task-B performance after the same waking interval. Importantly, the pattern of results indicates that the effect of task-A interference on task-B performance was not evident shortly after task-B was learned but rather required additional time awake to emerge. Moreover, though proactive interference is typically described as prior learning impeding the learning of new information or skills, the proactive interference observed here manifested as impaired subsequent retention of the new auditory classification rather than an impaired ability to learn the new classification. In both experiments, starlings that were trained sequentially on task-A and task-B tended to learn task-B better, not worse, than task-A, indicating that the learning of task-A may have enhanced task-B acquisition (Cai et al. 2016).

Humans and other animals acquire new information and skills each day, raising the potential for memory interference with each instance of learning. Examining these processes is thus critical for understanding how memories are formed and why they are forgotten (Wixted 2004, 2005; Altmann and Schunn 2012; Sadeh et al. 2014). In the present study, starlings that learned only one auditory classification task displayed no evidence of memory loss across the day, but starlings trained sequentially on two tasks showed clear retroactive and proactive interference between the tasks such that memory was impaired for both tasks. Yet, the two types of interference did not develop together. Rather, the retroactive interference of task-B on task-A was evident immediately after task-B was learned. In contrast, the emergence of proactive interference from task-A on task-B was delayed, only materializing after additional time awake. This asymmetric time

course of retroactive and proactive interference in the starlings shares similarities with earlier studies of interference in humans (Crowder 1976; Wixted and Rohrer 1993; Wixted 2004).

The pattern of immediate retroactive interference and delayed proactive interference observed here provides suggestions for understanding how interference between new memories develops. The data support a memory consolidation framework in which learning initiates a process to transform a newly encoded, labile memory engram into a more stable, long-term form (McGaugh 2000; Bailey et al. 2015; Squire et al. 2015). Though consolidation is thought to stabilize memories, the synaptic- and systems-level processes underlying consolidation require time (and often sleep), resulting in a post-encoding period when new memory traces are vulnerable to disruption. For the case of retroactive interference in experiment-1, task-A performance was impaired immediately after task-B training. This suggests that the learning of task-B interfered with the memories formed during task-A because task-B was acquired while the task-A engrams were labile. For the case of proactive interference in experiment-2, task-B performance was impaired after a delay rather than immediately after task-B training. This indicates that the proactive interference of task-A on task-B developed during the retention period while the memories for both task-A and task-B were labile, suggesting that the ongoing consolidation of the task-A memories interfered with the now labile task-B memories. In contrast, classification performance in the No-Interference conditions from both experiments remained stable across various retention periods. Although the new memories were labile during these periods, there was no memory disruption without an interfering task.

Consolidation theory provides a framework for when a memory may be vulnerable to interference, but the underlying causes of the interference remain an open question. Are encoding and consolidation competing states such that the encoding of a new memory takes priority over the consolidation of a similar memory? If so, the memory encoding of task-B could disrupt the simultaneous consolidation of task-A, leading to disrupted task-A engrams and impaired performance. Indeed, consolidation appears to be most efficient during sleep, a period when encoding demands are minimal (Rasch and Born 2013). Memory consolidation also entails time-dependent cascades of molecular processes, and consolidation is impaired when these are disrupted (McGaugh 2000; Izquierdo et al. 2006). Are different stages of these processes in conflict with each other such that the ongoing consolidation of one task (e.g., task-A) can interfere with a similar task (e.g., task-B) at a different stage of consolidation? Finally, is interference a consequence of similar memories being represented by overlapping neuronal ensembles? During task-A learning, neuronal ensembles would form associations between each task-A stimulus and its appropriate response. During task-B learning, additional associations would be formed between task-B sounds and responses. Some neurons in the task-A and task-B engrams might overlap because similar memories encoded closely in time tend to have overlapping representations (Rogerson et al. 2014; Cai et al. 2016). Moreover, since neurons are recruited to engrams based on their level of neuronal excitability immediately before training (Rogerson et al. 2014; Yiu et al. 2014), neurons that were excited during task-A could be preferentially recruited as members of the task-B ensembles. Consequently, overlapping representations could contribute to both retroactive and proactive interference if neurons that signal a “Go” response in one task also signal a “No-Go” response in the other task. Overall, determining the operating characteristics of interference in forgetting will require a wide range of approaches with diverse memory tasks and species. The current behavioral work represents an attractive comparative approach to further our understanding of how we remember and why we forget.

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