

Sleep Consolidation of Interfering Auditory Memories in Starlings

Timothy P. Brawn¹, Howard C. Nusbaum¹, and Daniel Margoliash^{1,2}

¹Department of Psychology and ²Department of Organismal Biology and Anatomy, University of Chicago

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Abstract

Memory consolidation has been described as a process to strengthen newly formed memories and to stabilize them against interference from similar learning experiences. Sleep facilitates memory consolidation in humans, improving memory performance and protecting against interference encountered after sleep. The European starling, a songbird, has also manifested sleep-dependent memory consolidation when trained on an auditory-classification task. Here, we examined how memory for two similar classification tasks is consolidated across waking and sleep in starlings. We demonstrated for the first time that the learning of each classification reliably interferes with the retention of the other classification across waking retention but that sleep enhances and stabilizes the memory of both classifications even after performance is impaired by interference. These observations demonstrate that sleep consolidation enhances retention of interfering experiences, facilitating opportunistic daytime learning and the subsequent formation of stable long-term memories.

Keywords

memory, sleep-wake cycle, comparative psychology, learning, forgetting

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Memory consolidation transforms newly acquired labile memories into stable memories resistant to subsequent forgetting (McGaugh, 2000). Sleep is widely implicated in human memory consolidation (Diekelmann, Wilhelm, & Born, 2009; Walker & Stickgold, 2006). For example, sleep benefits emotional memory (Hu, Stylos-Allan, & Walker, 2006; Payne, Stickgold, Swanberg, & Kensinger, 2008), affects false memory formation (Diekelmann, Born, & Wagner, 2010; Fenn, Gallo, Margoliash, Roediger, & Nusbaum, 2009), and promotes prospective memory (Scullin & McDaniel, 2010). Likewise, sleep consolidates learning of visual texture discrimination (Stickgold, James, & Hobson, 2000), motor-sequence learning (Brawn, Fenn, Nusbaum, & Margoliash, 2010; Korman et al., 2007; Walker, Brakefield, Hobson, & Stickgold, 2003), sensorimotor learning (Brawn, Fenn, Nusbaum, & Margoliash, 2008), and the perceptual learning of synthetic speech (Fenn, Nusbaum, & Margoliash, 2003). Studies of sleep-dependent consolidation have typically involved a single task, yet learning often entails the acquisition of similar skills or information that could interfere with each other. Consequently, investigating memory processing under conditions of interference is essential to understanding how memories are consolidated.

Few researchers have examined the interaction between interference and consolidation across waking and sleep. Experiments on associative word-pair learning have shown that sleep recovers memory of a given word-pair list from the retroactive interference of learning a second word-pair list before sleep (Drosopoulos, Schulze, Fischer, & Born, 2007) and reduces susceptibility to interference encountered after sleep (Ellenbogen, Hulbert, Jiang, & Stickgold, 2009; Ellenbogen, Hulbert, Stickgold, Dinges, & Thompson-Schill, 2006). An investigation of associative object-location learning found that memory reactivation (via a contextual odor cue) during a short waking period made object-location memories more susceptible to interference, whereas reactivation during a short sleep period stabilized performance against interference (Diekelmann, Büchel, Born, & Rasch, 2011). Whether sleep provides protection against interference remains an open question, however, because performance without the reactivation cue was nearly identical in the wake and sleep conditions.

Corresponding Author:

Timothy P. Brawn, University of Chicago, 1027 E. 57th St., Chicago, IL 60637

E-mail: tbrawn@uchicago.edu

Finally, studies of motor-sequence memory have found that learning a second sequence disrupts the sleep-dependent consolidation of the first sequence if the second sequence is learned within 2 hr of the first sequence but not after 6 hr (Korman et al., 2007; Walker et al., 2003), though these studies were influenced by confounding experimental procedures (Brawn, Fenn, et al., 2010; Rickard, Cai, Rieth, Jones, & Ard, 2008). Clearly, interference has a compelling effect on memory processing, but the interaction between sleep consolidation and interference remains unresolved.

Sleep has also been implicated in animal learning (Poe, Walsh, & Bjorness, 2010). Recently, we trained and tested European starlings on an auditory-classification task in an experiment modeled after sleep-memory studies in humans (Brawn, Nusbaum, & Margoliash, 2010; see the Supplemental Material available online). In this task, starlings learned to classify segments of novel starling songs and were retested after retention intervals that either consisted of wakefulness or included a night of sleep. Classification performance decreased nonsignificantly across waking retention but improved significantly after any retention interval that included sleep, which established a pattern of performance changes similar to that observed in human memory tasks. However, one notable difference between the starling and human results is that human task performance is often significantly reduced after waking retention (e.g., Brawn et al., 2008; Brawn, Fenn, et al., 2010; Ellenbogen et al., 2009; Ellenbogen et al., 2006; Fenn et al., 2003; Payne et al., 2008), yet the performance reduction in starlings failed to reach significance. This difference could reflect interference from the richer waking experience of humans because daytime behavior in human studies is not controlled, whereas starlings encountered only familiar baseline stimuli during wakefulness, which limited potential interference.

In the present study, we extended this classification paradigm to examine how learning a second classification affects consolidation of both the primary (Classification A) and interference (Classification B) tasks. Our experiments were designed to answer four questions concerning how the memory representations of the primary and interference tasks interact across waking and sleeping retention. First, does one learning experience interfere with the retention of another similar learning experience across wakefulness? That is, does learning Classification B impair the retention of Classification A (retroactive interference), and does learning Classification A impair the retention of Classification B (proactive interference)? Second, is the timing of the interference critical to its effect on memory consolidation? Specifically, are the effects of interference different if training on Task B begins immediately after training on Task A or 4 hr later? Third, does sleep consolidate learning even after starlings encounter interference or does interference disrupt sleep-dependent consolidation? That is, will postsleep classification performance be impaired in conditions in which interference is encountered compared with conditions in which only a single classification is learned? Finally, does sleep reduce susceptibility to

interference encountered after sleep such that learning Classification B after a period of sleep does not interfere with performance on Classification A?

Experiment I

Method

Participants. Twenty-four adult European starlings (*Sturnus vulgaris*) were maintained on a 24-hr schedule consisting of 16 hr of light and 8 hr of darkness.

Stimuli. Thirteen novel stimulus pairs, each consisting of two 5-s segments of natural starling song, were recorded from 13 starlings. One pair was used in a practice session before the experimental sessions, and the other 12 pairs were used in seven experimental conditions. A baseline stimulus pair in which one stimulus consisted of a rising tone and the other consisted of a falling tone was used in the baseline classification task.

Procedure. Starlings completed an auditory-classification task based on a go/no-go operant procedure (Brawn, Nusbaum, & Margoliash, 2010). Birds initiated stimulus playback by probing a response port with their beak and had 2 s after stimulus completion to probe a second response port or withhold response. During each 2.5-hr training session, starlings could complete up to 270 trials. Responses to one stimulus (go) produced a 2-s food reward; responses to the other stimulus (no-go) resulted in a 20-s lights-out punishment. Nothing occurred if starlings withheld response. The stimulus for each trial was selected randomly, except that the same stimulus was selected for the next trial whenever a starling responded incorrectly, up to five consecutive times. After training, starlings received 15 min of free access to food. During each 30-min testing session, starlings could complete up to 30 trials. During the test session, responses to the go stimulus produced a 2-s food reward, and responses to the no-go stimulus resulted in a 10-s lights-out period. The stimulus for each test trial was selected randomly, with the constraint that each stimulus was selected five times for every 10 trials.

Each starling became familiar with the go/no-go procedure by performing a baseline classification task with the baseline stimulus pair before starting the experimental conditions. Starlings were also engaged in the baseline task whenever they were not completing training or testing sessions. Additionally, all starlings underwent a familiarization practice session by completing a training session with the practice stimulus pair from 7:45 to 9:45 a.m., followed by test sessions at 10:00 a.m., 2:30 p.m., and 7:00 p.m. for 2 days.

Experimental design. Each starling participated in seven experimental conditions (Fig. 1) that followed an A-B-A (five interference conditions) or A-A (two control conditions) design, with three nights of sleep separating each condition. In the wake-retention sessions, starlings were trained and tested

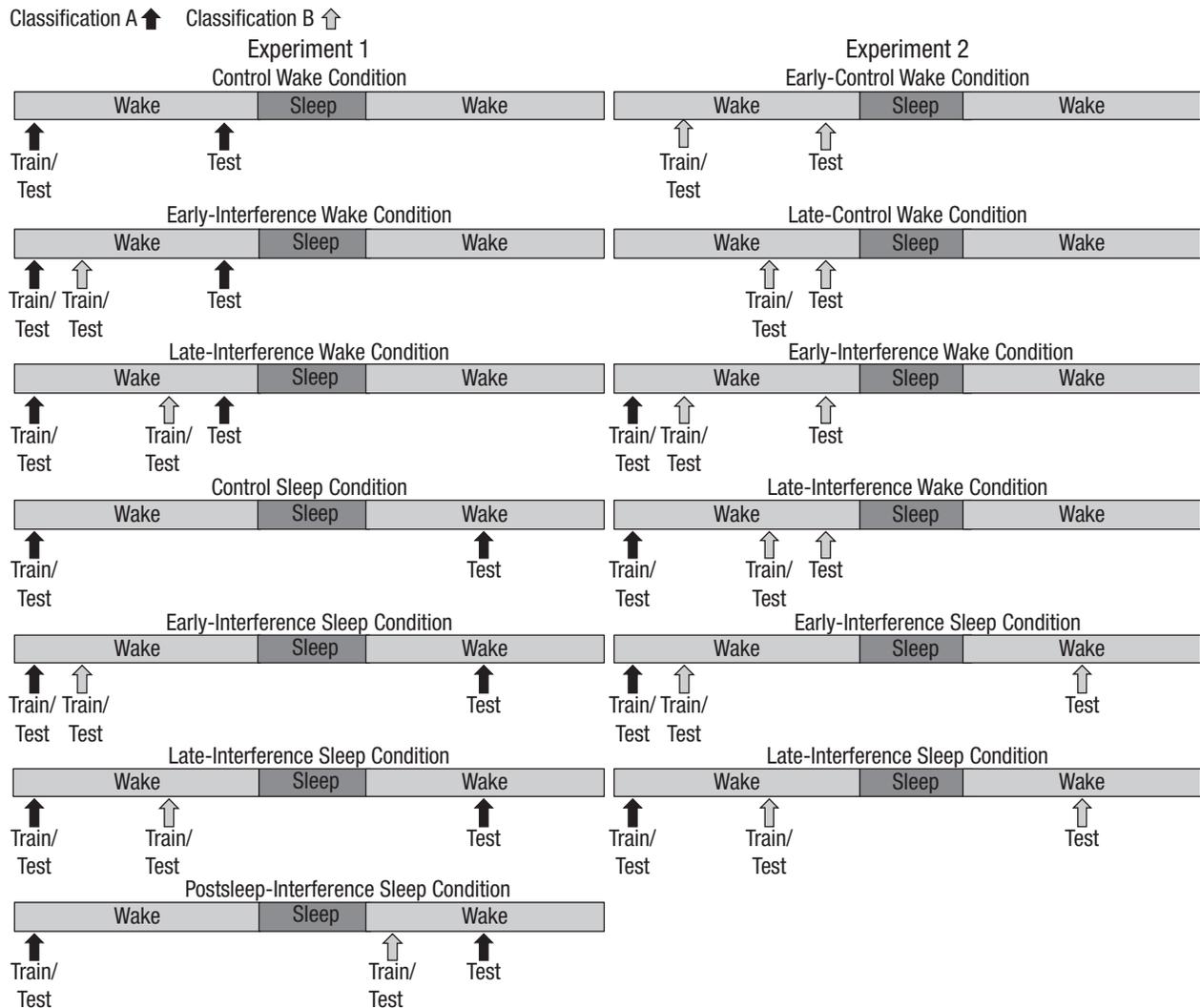


Fig. 1. Conditions in the two experiments. Starlings were tested on their accuracy at classifying stimuli at variable intervals after periods of wakefulness or sleep. In Experiment 1, testing on Classification A occurred twice, either without intervening training (control conditions) or with intervening training on Classification B (interference conditions). In the wake conditions, all testing occurred before sleep. In the sleep conditions, the second testing of Classification A took place after a period of sleep. In the interference conditions, training on Classification B occurred either soon after initial testing of Classification A (early conditions) or 4 hr later (late conditions). In Experiment 2, testing on Classification B occurred twice, either without training on Classification A (control conditions) or with preceding training on Classification A (interference conditions). Initial testing on Classification B occurred either early in the first period of wakefulness or closer in time to the second test.

on Classification A in the morning and retested at 7:00 p.m. on the same day. Starlings were additionally trained and tested on Classification B (a different pair of novel song segments) immediately after completing the Classification A test session (early interference) or 4 hr later (late interference). In the sleep-retention sessions, starlings were trained and tested on Classification A in the morning and retested at 12:00 p.m. on the following day. Starlings were also trained and tested on Classification B immediately after completing the Classification A test session (early interference), 4 hr later (late interference), or on the next morning prior to the postretention test (postsleep interference). Two control conditions (wake and sleep), in which starlings did not receive training on Classification B, were also included. The retention intervals for the

wake and sleep conditions differed because of exigencies of the experimental procedures (see the Supplemental Material). The three wake-retention conditions were completed first, followed by the four sleep-retention conditions, but each starling completed the seven conditions in a unique order. The stimulus pairs used in each condition were assigned randomly for each bird.

Performance measures. Performance was measured as the percentage of correct trials during a test session; a correct trial entailed responding to a go stimulus or withholding response to a no-go stimulus. Performance on the first 50 baseline trials after each test session was also measured as a control for potential circadian confounds.

Statistical analyses. One- and two-way repeated measures analyses of variance (ANOVAs) were used to assess differences in classification accuracy and performance changes across the tests and conditions. Specific comparisons were analyzed using t tests with Holm's Bonferroni procedure to correct for multiple comparisons. One-sample t tests were used to verify that posttraining classification accuracy was greater than chance performance.

Results

Performance accuracy on the posttraining Classification A test averaged across all conditions was 68.1% ($SEM = 1.7\%$). This performance level was significantly greater than chance performance of 50%, $t(23) = 10.55$, $p < .0001$, which confirms that a single training session produced significant auditory-classification learning in the starlings. Having learned Classification A, starlings also learned the second classification task. Performance accuracy on the posttraining Classification B test averaged across the five interference conditions was 67.6% ($SEM = 1.8\%$), which was also significantly above chance, $t(23) = 10.05$, $p < .0001$. Posttraining test performance for each task did not differ across the conditions—Classification A: $F(6, 138) = 0.57$, $p = .75$; Classification B: $F(4, 92) = 1.69$, $p = .16$.

To evaluate performance on Classification A following training and retention, we conducted a 2 (test: posttraining, postretention) \times 7 (condition: control wake, early-interference wake, late-interference wake, control sleep, early-interference sleep, late-interference sleep, postsleep-interference sleep) repeated measures ANOVA. Although there were no main effects of test, $F(1, 23) = 1.15$, $p = .29$, or condition, $F(6, 138) = 1.02$, $p = .42$, a significant Test \times Condition interaction was obtained, $F(6, 138) = 10.0$, $p < .0001$ (Fig. 2a). Task A classification performance in the control wake condition decreased by 1.7 percentage points ($SEM = 1.6$) from the posttraining to the postretention test, which represents a non-significant performance reduction, $t(138) = 1.24$, $p = .22$. By comparison, the early-interference wake and late-interference wake conditions (in which Task B interference occurred after Task A training during wakefulness) showed significant performance losses from the posttraining to the postretention test of 8.5 percentage points ($SEM = 1.6$), $t(138) = 6.38$, $p < .001$, and 5.8 percentage points ($SEM = 1.8$), $t(138) = 4.32$, $p < .001$, respectively. In contrast, classification performance improved significantly for each condition that included sleep. Performance in the control sleep condition improved by 5.9 percentage points ($SEM = 1.9$), $t(138) = 4.42$, $p < .001$. Critically, the three sleep interference conditions (in which the postretention test occurred after a period of sleep) showed improvements of 4.3 percentage points ($SEM = 2.1$), $t(138) = 3.22$, $p < .01$ (early-interference sleep condition), 5.8 percentage points ($SEM = 1.7$), $t(138) = 4.35$, $p < .001$ (late-interference sleep condition), and 4.5 percentage points ($SEM = 2.1$), $t(138) = 3.36$, $p < .01$ (postsleep-interference sleep condition).

A one-way repeated measures ANOVA on the performance-improvement scores revealed significant differences across conditions, $F(6, 138) = 10.0$, $p < .0001$ (Fig. 3a). We therefore tested specific comparisons to assess the effects of interference on classification performance across retention during waking and sleeping. There were no significant differences between the early-interference wake and late-interference wake conditions, $t(138) = 1.45$, $p = .15$, or between the early-interference sleep and late-interference sleep conditions, $t(138) = 0.80$, $p = .43$. Likewise, performance in the postsleep-interference sleep condition, which received interference training after sleep, was not different from performance in the sleep conditions that encountered interference before sleep (early- and late-interference sleep conditions), $t(138) = 0.36$, $p = .72$. These results suggest that the timing of learning Classification B was not critical to its effect on Classification A.

A comparison of the control wake and control sleep conditions verified that sleep, in the absence of interference, produced significantly greater performance improvement than wakefulness, $t(138) = 4.01$, $p < .001$. In contrast, performance in the early- and late-interference wake conditions was significantly reduced compared with performance in the control wake condition, $t(138) = 3.56$, $p < .01$, which demonstrates that learning Classification B interfered with the memory of Classification A across waking retention. However, sleep consolidated Classification A despite Task B interference. Although the sleep-interference conditions showed significantly greater performance improvement than the wake interference conditions, $t(138) = 10.14$, $p < .001$, there was no difference between the sleep interference and control sleep conditions, $t(138) = 0.78$, $p = .43$, which indicates that Task A performance was restored to a level comparable with a condition in which interference was not encountered. An analysis of performance on the baseline classification task after each test session suggests that the beneficial effect of sleep on auditory-classification memory cannot be explained by circadian factors on performance (see the Supplemental Material).

Experiment 2

The results from Experiment 1 suggest two conclusions: learning Classification B interfered with Classification A across waking retention, and sleep consolidated memory for Classification A despite interference from Classification B. However, it is unclear whether memory for Classification B was also consolidated. Does learning Classification A also impair memory retention for Classification B across wakefulness even though Classification A was learned before Classification B? Is Classification B also consolidated by sleep, or does sleep consolidate some learning (e.g., Classification A) at the expense of other learning (e.g., Classification B)? To address these questions, we conducted a second experiment in which performance on Classification B rather than on Classification A was retested after waking and sleeping retention.

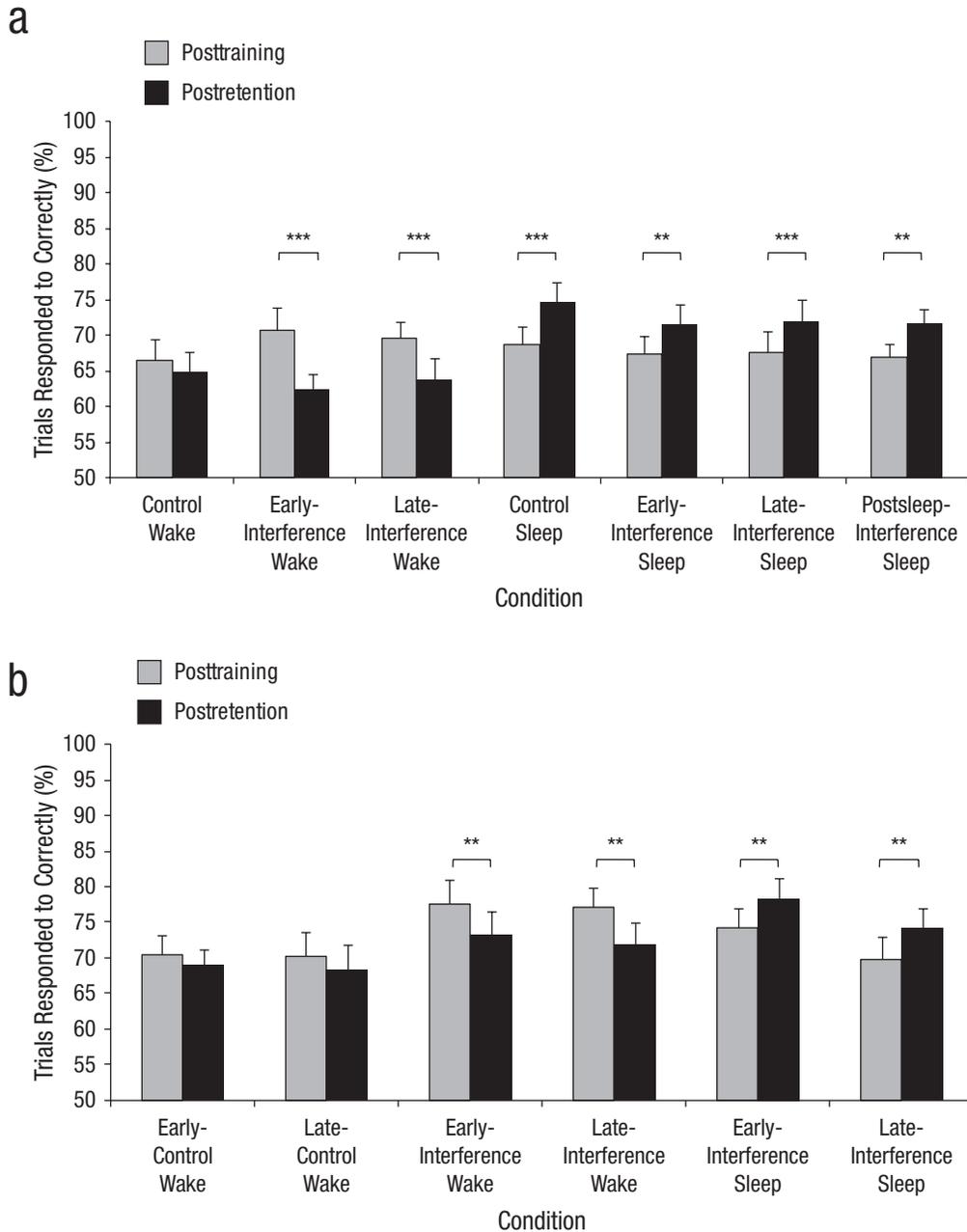


Fig. 2. Mean accuracy in (a) Experiment 1 and (b) Experiment 2. The percentage of trials responded to correctly in the posttraining and postretention tests is shown for each condition. Asterisks indicate significant differences between results at the two test times (** $p < .01$; *** $p < .001$). Error bars show standard errors of the mean.

Method

Twenty-four new starlings were maintained on a 24-hr schedule consisting of 16 hr of light and 8 hr of darkness. The stimuli, procedures, performance measures, and statistical analyses were identical to those used in Experiment 1. However, the conditions differed slightly: Each starling participated in six experimental conditions (Fig. 1) that followed an A-B-B (four interference conditions) or B-B (two control conditions) design. In the early-interference conditions, starlings were

trained and tested on Classification A in the morning, and this training was immediately followed by training and testing on Classification B. Starlings in the early-interference wake condition were retested on Classification B at 7:00 p.m. the same day, and starlings in the early-interference sleep condition were retested on Classification B at 12:00 p.m. the next day. In the late-interference conditions, starlings were trained and tested on Classification A in the morning, followed by training and testing on Classification B beginning 4 hr later. Starlings in the late-interference wake condition were retested on

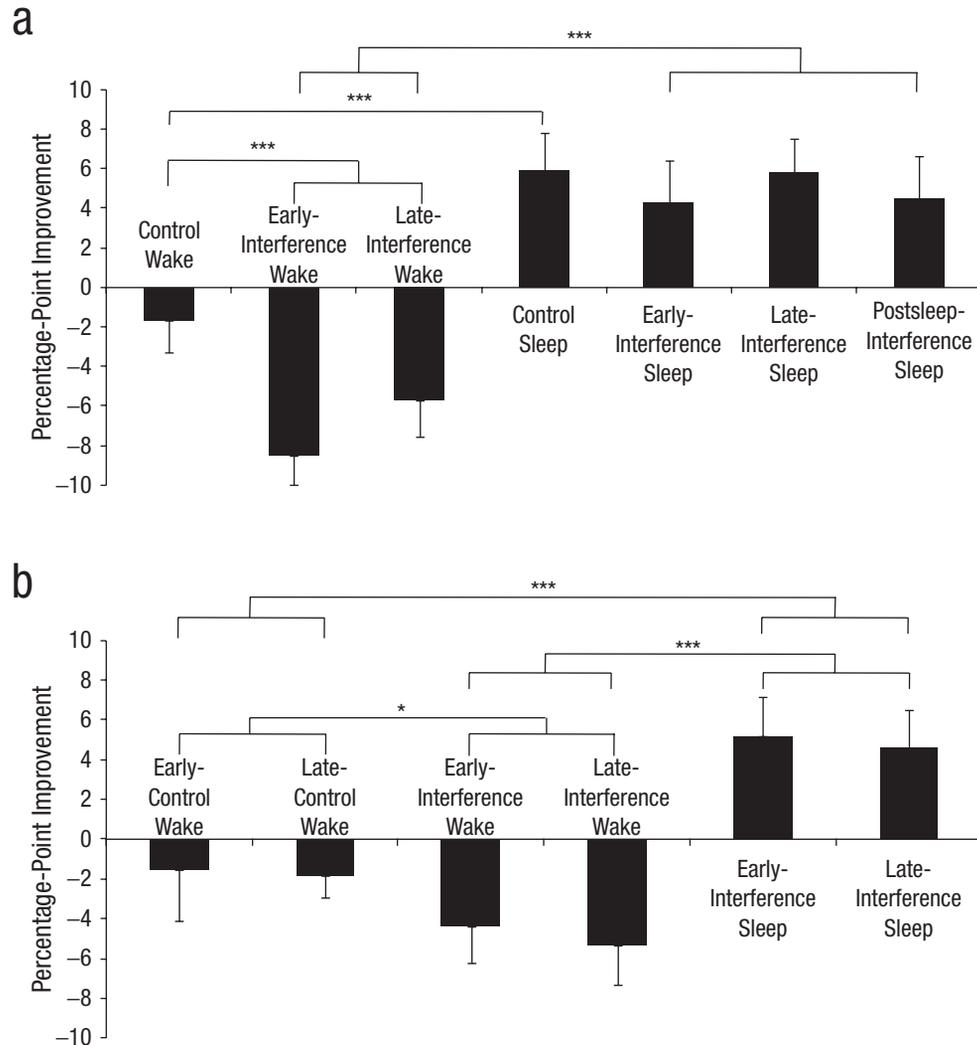


Fig. 3. Mean performance improvement in (a) Experiment 1 and (b) Experiment 2. The percentage-point improvement is shown as a function of condition. Asterisks indicate significant differences between conditions (* $p < .05$; *** $p < .001$). Error bars show standard errors of the mean.

Classification B at 7:00 p.m. the same day, and starlings in the late-interference sleep condition were retested on Classification B at 12:00 p.m. the next day.

Starlings in two wake control conditions (early-control wake and late-control wake conditions), which did not learn Classification A, were trained and tested on Classification B at identical times as starlings in the two respective wake interference conditions (early- and late-interference wake conditions). Similar sleep control conditions were not tested because the control sleep condition from Experiment 1 and several conditions from prior work (Brawn, Nusbaum, & Margoliash, 2010) have consistently shown that sleep improves performance after starlings learn a single auditory-classification task.

Results

As in Experiment 1, a single training session produced learning on the posttraining classification tests that was significantly

above chance. Performance accuracy averaged across all conditions on the posttraining Classification B test was 73.2% ($SEM = 2.0\%$), $t(23) = 11.46$, $p < .0001$. Likewise, performance accuracy averaged across the four interference conditions on the posttraining Classification A test was 69.6% ($SEM = 2.0\%$), $t(23) = 9.74$, $p < .0001$. Posttraining test performance for each task did not differ across conditions—Classification B: $F(5, 115) = 1.78$, $p = .12$; Classification A: $F(3, 69) = 1.96$, $p = .13$.

To evaluate performance on Classification B, we conducted a 2 (test: posttraining, postretention) \times 6 (condition: early-control wake, late-control wake, early-interference wake, late-interference wake, early-interference sleep, late-interference sleep) repeated measures ANOVA. There were no main effects of test, $F(1, 23) = 1.01$, $p = .33$, or condition, $F(5, 115) = 1.70$, $p = .14$, but a significant Test \times Condition interaction was obtained, $F(5, 115) = 4.40$, $p < .01$ (Fig. 2b). Performance accuracy for Task B in the early-control wake and late-control

wake conditions decreased nonsignificantly by 1.5 percentage points ($SEM = 2.6$), $t(115) = 1.08$, $p = .30$, and 1.7 percentage points ($SEM = 1.1$), $t(115) = 1.24$, $p = .23$, respectively. By comparison, performance in the early-interference wake and late-interference wake conditions, in which Classification A was learned prior to Classification B, showed significant performance losses of 4.4 percentage points ($SEM = 1.8$), $t(115) = 3.09$, $p < .01$, and 5.3 percentage points ($SEM = 2.0$), $t(115) = 3.77$, $p < .01$, respectively. Nonetheless, performance in the early-interference sleep and late-interference sleep conditions displayed significant improvements of 4.3 percentage points ($SEM = 2.0$), $t(115) = 3.06$, $p < .01$, and 4.6 percentage points ($SEM = 1.9$), $t(115) = 3.23$, $p < .01$, respectively.

A one-way repeated measures ANOVA on performance-improvement scores revealed significant differences across conditions, $F(5, 115) = 4.40$, $p < .01$ (Fig. 3b). Posttests determined that there were no significant differences between scores in the early-control wake and late-control wake conditions, $t(115) = .11$, $p = .91$, between scores in the early-interference wake and late-interference wake conditions, $t(115) = 0.48$, $p = .64$, or between scores in the early-interference sleep and late-interference sleep conditions, $t(115) = 0.11$, $p = .86$. However, performance in the wake interference conditions was significantly worse than performance in the wake control conditions, $t(115) = 2.28$, $p < .05$, which demonstrates that learning Classification A in the morning impaired retention of Classification B across wakefulness. Furthermore, performance improvement in the sleep interference conditions was significantly greater than in both the wake interference conditions, $t(115) = 6.49$, $p < .001$, and the wake control conditions, $t(115) = 4.22$, $p < .001$, which indicates that sleep also consolidated memory for Classification B. As in Experiment 1, this pattern of memory loss across waking retention and memory improvement across sleeping retention was not due to circadian factors on performance (see the Supplemental Material).

Discussion

In the two experiments reported here, we found that learning two similar classification tasks impaired starlings' performance on both classifications after a waking retention interval, but sleep eliminated this interference and consolidated learning for both tasks. Classification accuracy underwent a nonsignificant decline across waking retention in the absence of interference. This was consistent across three control conditions with retention intervals of 1 hr (late-control wake condition in Experiment 2), 5 hr (early-control wake condition in Experiment 2), and 9 hr (control wake condition in Experiment 1). Learning a second classification task, however, manifested retroactive and proactive interference, which resulted in significant impairments on both classification tasks. This highlights interference, rather than memory decay, as the cause of the starlings' performance loss and suggests interference as the source of waking performance reductions that are often observed in human studies (e.g., Brawn et al., 2008;

Brawn, Fenn, et al., 2010; Ellenbogen et al., 2009; Ellenbogen et al., 2006; Fenn et al., 2003; Payne et al., 2008).

Given that each of the two tasks interfered with the retention of the other task during the day, how does sleep consolidate learning in the presence of such interference? Sleep could have restored performance for one task by strengthening the representation of that task or by weakening the representation of the other task. Alternatively, the interference between the tasks could have disrupted the sleep-dependent consolidation of both tasks. Yet sleep consolidated the memory of both classifications. Performance improved significantly after sleep without interference. Likewise, starlings in four conditions that encountered interference before sleep (early-interference sleep and late-interference sleep in Experiment 1 and early-interference sleep and late-interference sleep in Experiment 2) displayed significant improvements after sleep, which demonstrates that sleep restored and enhanced classification memory. Additionally, interference encountered after sleep (in the post-sleep-interference sleep condition in Experiment 1) had no effect on the previous day's learning, which indicates that sleep protected classification memory from subsequent interference. The inclusion of interference in the auditory-classification paradigm actually magnified the memory benefit of sleep. Although interference increased performance loss across wakefulness, postsleep performance was no different than performance in the control conditions. This produced a greater sleep-dependent benefit for the interference conditions, which is comparable with the effect of interference on human declarative memory (Ellenbogen et al., 2009; Ellenbogen et al., 2006).

We have argued that sleep is responsible for the postsleep performance benefits observed in starlings. Exigencies of the animal experiments required retention intervals of up to 9 hr for the wake conditions compared with up to 26 hr for the sleep conditions, which leaves open the possibility of a time-dependent rather than sleep-dependent mechanism to explain the consolidation. However, we previously found that starlings that learn a single classification task express a nonsignificant performance decline from morning to evening but a significant improvement from evening to the next morning (Brawn, Nusbaum, & Margoliash, 2010; see the Supplemental Material); this finding demonstrates memory benefits after sleep in conditions with more comparable retention intervals. Furthermore, a multitude of human studies using equivalent 12-hr retention intervals for both wake and sleep conditions has consistently uncovered performance benefits after sleeping compared with waking retention (e.g., Diekelmann et al., 2009; Walker & Stickgold, 2006), which shows that sleep, and not time, is critical to consolidation. Nap studies have found that performance benefits can emerge after shorter, daytime retention periods if they include sleep (e.g., Korman et al., 2007; Mednick, Nakayama, & Stickgold, 2003; Nishida & Walker, 2007), which indicates that the occurrence of sleep rather than the passage of time contributes to consolidation. Additionally, consolidation is impaired if participants are deprived of sleep

on the first night after training (e.g., Fischer, Nitschke, Melchert, Erdmann, & Born, 2005; Gais, Lucas, & Born, 2006; Stickgold et al., 2000), which helps to refute the time-dependent hypothesis because memory should benefit even during sleep deprivation if the passage of time, and not sleep, is responsible for consolidation.

The present study demonstrated that sleep restores performance after retroactive and proactive interference and makes learning robust against interference encountered after sleep. This process is critical to the formation of stable long-term memories, and it raises questions as to what mechanism can account for these effects. Mechanistic explanations of memory consolidation generally focus on the strengthening of some memories or the weakening of others with the net result of an increased signal-to-noise ratio for memory retrieval. The synaptic homeostasis hypothesis (Tononi & Cirelli, 2003, 2006) would suggest that synapses involved in the acquisition of Tasks A and B become strengthened as the starlings learn each classification. Interference, in the form of weak synaptic connections due to stimulus or behavioral-response similarities, could develop between neural representations of the two classification tasks. Synapses would then be downscaled, or reduced in strength, during slow-wave sleep, which could eliminate interference by reducing crosstalk between the two tasks. Additionally, memories could be strengthened during sleep by reactivation of the neural representations of the tasks. Reactivation could provide a form of off-line rehearsal or reorganize the newly formed memory traces during transfer from temporary to long-term storage during sleep (O'Neill, Pleydell-Bouverie, Dupret, & Csicsvari, 2010; Rasch & Born, 2007).

Though species-specific or task-related differences in sleep-dependent mechanisms of consolidation are possible, both synaptic homeostasis and neural reactivation are plausible explanations for the sleep-dependent memory benefits observed in starlings. Avian slow-wave sleep, as in mammals, is regulated by a homeostatic process (Rattenborg, Martinez-Gonzalez, & Lesku, 2009), and sleep in zebra finches contains a suite of characteristics similar to those observed in mammalian sleep (Low, Shank, Sejnowski, & Margoliash, 2008). Though studies of sleep reactivation have not been conducted in starlings, reactivation during sleep has been observed in adult zebra finches (Dave & Margoliash, 2000), and sleep-dependent changes in neural activity have been associated with song learning in juvenile zebra finches (Shank & Margoliash, 2009). Because this starling-classification paradigm is amenable to neurophysiological manipulations, future studies will have the potential to connect the behavioral benefits of sleep to the underlying mechanisms mediating sleep-dependent memory consolidation. The similar pattern of memory consolidation in starlings (for auditory-classification learning) and humans (for a multitude of procedural and declarative-memory tasks) across waking and sleeping retention, coupled with the similarities between mammalian and

avian sleep, suggest investigations of avian sleep and memory as an attractive comparative approach to understanding human memory consolidation.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at <http://pss.sagepub.com/content/by/supplemental-data>

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