The Impact of Napping on Memory for Future-Relevant Stimuli: Prioritization Among Multiple Salience Cues

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Prior research has demonstrated that sleep enhances memory for future-relevant information, including memory for information that is salient due to emotion, reward, or knowledge of a later memory test. Although sleep has been shown to prioritize information with any of these characteristics, the present study investigates the novel question of how sleep prioritizes information when multiple salience cues exist. Participants encoded scenes that were future-relevant based on emotion (emotional vs. neutral), reward (rewarded vs. unrewarded), and instructed learning (intentionally vs. incidentally encoded), preceding a delay consisting of a nap, an equivalent time period spent awake, or a nap followed by wakefulness (to control for effects of interference). Recognition testing revealed that when multiple dimensions of future relevance co-occur, sleep prioritizes top-down, goal-directed cues (instructed learning, and to a lesser degree, reward) over bottom-up, stimulus-driven characteristics (emotion). Further, results showed that these factors interact; the effect of a nap on intentionally encoded information was especially strong for neutral (relative to emotional) information, suggesting that once one cue for future relevance is present, there are diminishing returns with additional cues. Sleep may binarize information based on whether it is future-relevant or not, preferentially consolidating memory for the former category. Potential neural mechanisms underlying these selective effects and the implications of this research for educational and vocational domains are discussed.

Keywords: emotion, consolidation, memory, reward, sleep

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been shown to lead to enhanced performance following sleep using declarative (Wilhelm et al., 2011), procedural motor (Wilhelm et al., 2011), and visuospatial tasks (Van Dongen, Thielen, Takashima, Barth, & Fernández, 2012; Wilhelm et al., 2011). Together, these findings highlight that there are multiple prioritization cues that lead to preferential consolidation during sleep, some of which are inherently tied to the stimulus content (e.g., emotion) and others that are tied to stimulus associations (e.g., reward) or task goals (e.g., retrieval expectancy). In other words, future relevance is sometimes due to bottom-up, stimulus-driven characteristics of the stimuli (e.g., emotion), while other times it is due to top-down, goal-directed motivations that are present at the time of encoding (e.g., reward) or at the time of retrieval (e.g., intentionality of encoding).

It has been postulated that there may be a common mechanism supporting the prioritization of these different types of information. Particularly, the mechanism of reactivation, in which experienced events are “replayed” during sleep, has been suggested to underlie not only sleep-dependent consolidation as a whole (e.g., reexperienced events are “replayed” during sleep, has been suggested to support the prioritization of these different types of information), but also to underlie sleep’s selective effects on consolidation (e.g., see Bennion, Payne, & Kensinger, 2015, for review; alternatively, see synaptic homeostasis hypothesis; Tononi & Cirelli, 2006). Supporting this idea, animal research has shown that rewarded information is replayed in the hippocampus and ventral striatum in rats during sleep (Lansink et al., 2008; Lansink, Goltstein, Lankelma, McNaughton, & Pennartz, 2009), and that hippocampal CA3 neurons are significantly more active during sharp wave ripples following reward relative to not receiving a reward (Singer & Frank, 2009).

To directly investigate similar questions in humans, Oudiette, Antony, Creery, and Paller (2013) have used a targeted memory reactivation paradigm, in which participants learn object-location associations while hearing corresponding sounds. Because slow waves are suggested to facilitate hippocampal-neocortical interactions and memory reactivation (Mölle & Born, 2011), the experimenter replays these sounds during slow-wave sleep, later assessing how such reactivation affects performance on a subsequent memory test. In one study that investigated the effects of targeted memory reactivation on high-value versus low-value associations, recall accuracy for reactivated object-location associations was better for high-relative to low-value associations (Oudiette, Antony, Creery, & Paller, 2013). As such, Oudiette et al. (2013) have suggested that important memories, as determined by “emotional salience, intention to remember, novelty, reward, explicit instruction” (p. 147) and more, are selectively replayed during sleep, thus leading to their enhanced consolidation during wake. Or in other words, reactivation likely underlies sleep’s selective consolidation of future-relevant information.

Despite this proposal of a common mechanism for information that has future utility, the majority of prior research has investigated how sleep affects emotional, rewarded, and to-be-tested information separately. While each of these cue types has been shown to lead to preferential sleep-dependent consolidation when it is the only cue for future relevance, the present study seeks to understand how the prioritization of information takes place when multiple cues for future relevance (i.e., emotion, reward, instructed learning) co-occur. Not only does this design mirror real-world situations, when these signals of future relevance overlap (Stickgold, 2013), but it also allows for an examination of how sleep weights different cues for future relevance. We addressed two key questions: First, would there continue to be beneficial effects of sleep for each of these cue types, or might one type of cue dominate? Second, would there be evidence of an interaction between the factors?

When considering how the factors would interact, there were two possible outcomes: supra-additive or sub-additive interactions. A supraadditive interaction would suggest that sleep preferentially consolidates information that has multiple cues for future relevance. This possibility is supported by research demonstrating that the sleep-dependent gain in performance of a motor sequence task is greater for sequences that had been associated with monetary reward versus no monetary reward at training (Fischer & Born, 2009). Here, it could be argued that the two dimensions of future relevance (i.e., the expectation of a later test and monetary reward) were additive, resulting in greater performance following sleep than if only one dimension of future relevance had been present. However, as there was no condition in which participants did not expect a memory test, there is no way to be certain of this. It is plausible that there is a limit to the extent to which the addition of future-relevant cues can further enhance consolidation. For instance, there may be subadditive interactions between future-relevant cues, such that once one cue is present, there are diminishing returns associated with the presence of additional cues. This possibility is supported by research demonstrating that participants who were instructed to memorize words associated with different point values had better memory following sleep relative to wake, but this did not depend on point value (Baran, Daniels, & Spencer, 2013). Similarly, in a study in which participants encoded a series of images composed of a negative foreground object on a neutral background preceding a night of sleep, their selective enhancement of emotional components of a memory was comparable regardless of whether participants were informed of the upcoming test prior to sleep (Cunningham et al., 2014). Both of these studies suggest that once information is identified as important (e.g., whether due to expectation of a future test or emotional salience), additional salience cues do not further improve memory following sleep.

These results would imply that sleep binarizes information into that which is, or is not, future-relevant, preferentially consolidating the former category.

In elucidating sleep’s selective effects on memory for some stimuli over others, it is also important to understand the time course over which this occurs. The majority of research on sleep and memory consolidation has utilized overnight delays consisting of a full night of sleep between encoding and retrieval. Those that have used shorter delays (i.e., a daytime nap) have shown comparable effects to those of overnight sleep but in most cases have used incidental encoding tasks (i.e., those in which participants do not know their memory will later be tested; e.g., Alger, Lau, & Fishbein, 2010; Backhaus & Junghanns, 2006; Payne et al., 2015; Tucker et al., 2006). In seeking to understand the effects of sleep on memory for information that participants know will be tested, a nap design is particularly useful because instructed learning may be particularly likely to modulate memory after a short relative to long delay. For instance, participants may be more likely to believe that their efforts to remember information over 2 hr (a proximal goal) will successfully impact their performance, whereas memory after 12 hr (a more distal goal) may seem less attainable and relatively outside the participants’ control. As success expectancy
has been shown to relate to performance (Garland, 1984), using a nap design may exacerbate the effects of instructed learning on memory. This, however, may also depend on the stimuli, as Lo, Dijk, and Groeger (2014) showed that a daytime nap and overnight sleep had comparable effects on consolidation of unrelated word pairs that participants knew would be tested, but that the effect of overnight sleep was stronger for related pairs.

Together, the present study seeks to elucidate how a nap prioritizes information for consolidation when multiple salience cues exist within the same stimuli. While prior literature has investigated the effects of sleep on emotion, reward, and instructed learning separately, gaining a true understanding of how sleep affects memory in the real world (e.g., witnessing a crime and trying to remember details of the perpetrator involved) necessitates that these factors be investigated in conjunction with one another. The present study seeks to do so, testing the effects of a nap on memory for information that is salient due to bottom-up characteristics, top-down characteristics, or both.

Materials and Method

Participants

Participants were 84 native English speakers with normal or corrected-to-normal vision. The 74 used here (18- to 27-years-old, \( M = 20.3 \)) are those who scored above chance (hits minus false alarms) in memory performance averaged across stimuli valence. All participants were screened for neurological, psychiatric, and sleep disorders, and for medications affecting the central nervous system or sleep architecture. Participants were required to sleep for at least 7 hr a night and be in bed by 2:00 a.m. for the 5 nights leading up to the study, as verified by self-report questionnaire. Informed consent was obtained in a manner approved by the Boston College Institutional Review Board. Participants were initially randomly assigned to one of two groups, Nap or Wake, which were scheduled simultaneously. Another group of participants (Nap + Wake) was subsequently scheduled, which included a nap followed by an equivalent period of time spent awake between encoding and retrieval; this group was included to minimize concerns that any beneficial effects of a nap on memory performance in the Nap group were simply due to a lack of interference relative to the Wake group.

Conditions

The present study included participants in the Nap (24 participants; 12 female), Wake (24 participants; 12 female), and Nap + Wake groups (26 participants; 13 female). Participants in these groups were matched on a number of factors, including age (\( p = .09 \)), and scores on the Beck Depression Inventory (BDI; Beck & Beamesderfer, 1974; \( p = .24 \)), Beck Anxiety Inventory (BAI; Beck, Epstein, Brown, & Steer, 1988; \( p = .81 \)), and Morningness-Eveningness Questionnaire (MEQ; Horne & Ostberg, 1976; \( p = .11 \)). The Nap and Wake participants viewed the stimuli between 11 a.m. and 1 p.m., and were tested 2 hr after encoding. The Nap participants took a nap in the Boston College sleep laboratory during this delay interval, while the Wake participants stayed awake doing quiet, monitored activities within the lab. Participants in the Nap + Wake condition slept for a 2-hr period immediately following encoding and then had a 2-hr wake period in which they did quiet, monitored activities within the lab. See supplemental Figure 1a for a depiction of the timing of the procedure for each group.

Encoding Procedure

Stimuli. During each encoding block (see Incidental versus intentional encoding section), participants studied 90 composite scenes for four seconds each. These scenes were composed of a negative, positive, or neutral item (30 of each valence) superimposed on a plausible neutral background, such that each version of the scene could theoretically be observed in real life. For instance, an avenue would be a plausible neutral background for a taxi cab (neutral), taxi cab accident (negative), and a parade float (positive). The negative and neutral items had been previously rated for valence and arousal (1 = low; 7 = high), with negative items rated as highly arousing and low in valence (arousal >5; valence <3) and neutral items rated as nonarousing and neutral in valence (arousal <4; valence: 3–5; Bennion, Mickley Steinmetz, Kensinger, & Payne, 2014, 2015; Kensinger, Garoff-Eaton, & Schacter, 2007; Waring & Kensinger, 2009). During pilot testing for the present study, positive items were rated as highly arousing and high in valence (arousal >5; valence >5).

Incidental versus intentional encoding. Encoding was separated into two blocks. The first block was an incidental encoding block, in which participants did not know that their memory for the stimuli would later be tested. The second block was an instructed (intentional) encoding block, in which participants were instructed to remember the stimuli with knowledge of a later memory test. The order of these blocks could not be counterbalanced because it was important that participants did not speculate during the incidental encoding block that there would be a later memory test; if the intentional encoding block occurred first, participants likely would have engaged with the stimuli differently during the subsequent incidental encoding block, possibly still expecting a memory test. During both blocks, participants engaged in the same deep encoding task in order to ensure that they were actively thinking about each scene. This task involved viewing the scene and making a distance judgment regarding how far away (in feet) they thought the photo was taken from. After having 4 s to view each scene, they had 3 s to make this multiple-choice distance judgment, indicating via keyboard press whether they believed the photo was taken from (a) less than 2 feet, (b) 2–5 feet, (c) 5–10 feet, or (d) greater than 10 feet away. See supplemental Figure 1b for a visual depiction of the encoding procedure.

Reward manipulation. Half of the scenes (45 per each block: 15 negative, 15 positive, 15 neutral) were rewarded while the other half were not rewarded (unrewarded). Rewarded versus unrewarded scenes were denoted by the color of the fixation cross (1-s duration) preceding the scene: A green fixation cross indicated that the subsequent scene would be rewarded, while a black fixation cross indicated that the subsequent scene would not be rewarded.

For the incidental encoding block, the reward was tied to the accuracy of the distance judgment that participants made about each scene. Specifically, they were told “For every correct distance judgment [for a rewarded scene], you will earn an additional entry into a raffle for a $100 Visa gift card.” In contrast, for the intentional encoding block, in which participants knew there
would be a later memory test, the reward was tied to their subsequent memory performance. They were told, “For each of the scenes that you remember during the memory test following the delay period, you will earn an additional entry into the raffle for the $100 Visa gift card.”

Delay Procedure
Following the encoding task, participants underwent a delay period consisting of a Nap, Wake, or Nap + Wake, depending on condition. All participants wore a Motionlogger sleep watch actigraph (similar to a wristwatch; Ambulatory Monitoring, Inc., Ardsley, NY), which uses an accelerometer to detect movement several times per second. Thus, the actigraph allowed us to determine participants’ nap duration (in the Nap and Nap + Wake groups) and to ensure that Wake participants did not fall asleep. The Nap + Wake participants also underwent polysomnography (PSG) during their nap in order to determine sleep stages, although PSG data were only used to establish from which stage of sleep participants were awakened. The length of the delay for Nap and Wake participants was 2 hr, while the length of the delay for Nap + Wake participants was 4 hr (first consisting of a 2-hr opportunity to nap, followed by a 2-hr opportunity to do quiet activities in the lab, including paper-and-pencil tasks associated with the study).

Recognition Procedure
Following the 2-hr (Nap and Wake conditions) or 4-hr (Nap + Wake condition) delay, participants performed a recognition task. They viewed items and backgrounds, presented separately and one at a time, and indicated whether each was “old” (included in a previously studied scene) or “new” (not previously studied). On the recognition test were the 180 old items (60 negative, 60 positive, 60 neutral) and the 180 old backgrounds (60 studied with a negative item, 60 studied with a positive item, 60 studied with a neutral item), intermixed with 180 new items (60 negative, 60 positive, 60 neutral) and 180 new backgrounds (by definition, all neutral). See supplemental Figure 1b for a visual depiction of the retrieval procedure. Analyses in the current study focus on participants’ memory for negative, positive, and neutral items as a function of whether the participant slept and of the intentionality or reward associated with that trial. See supplemental material for an additional analysis that investigates the variance accounted for by each future-relevant cue (i.e., emotion, intentionality, reward) within the groups that slept (Nap and Nap + Wake groups).

Results

Participants’ Sleep the Night Prior to the Study and During the Afternoon Nap
Sleep amount, as measured by self-report, was not significantly different between the three groups the night before retrieval (Nap: $M = 7.48$ hr, $SD = 1.99$; Wake: $M = 8.13$ hr, $SD = 1.22$; Nap + Wake: $M = 7.25$ hr, $SD = .76$, $F(2, 71) = 2.32, p = .11$). Further, including self-reported sleep duration the night before the study as a covariate in the subsequent analyses did not affect the significance of the results reported in this manuscript. Wake times on the day of the study also did not differ across groups (Nap: $8:57$ a.m. ± 56.6 min; Nap + Wake: $8:10$ a.m. ± 88.0 min; Wake: $8:50$ a.m. ± 87.1 min), $F(2, 71) = 2.64, p = .079$.

Sleep amount during the nap period, as measured by actigraphy, was equivalent between the Nap and Nap + Wake groups (Nap: $M = 89.9$ min, $SD = 18.9$ min; Nap + Wake: $M = 95.2$ min, $SD = 13.5$ min; $p = .22$). Wake after sleep onset (WASO) was $11.1 ± 12.9$ (Mean ± SD) minutes for the Nap group and $6.8 ± 6.9$ min for the Nap + Wake group, suggesting that participants largely remained asleep once they fell asleep. Of the Nap + Wake participants, who underwent PSG during their nap, the majority were awakened from light sleep (N1: 17%, N2: 61%) relative to slow-wave sleep (SWS; 9%) or REM sleep (REM; 13%).

Memory Performance by Group, Emotion, Intentionality, and Reward
To determine whether patterns of memory performance were comparable across negative and positive stimuli, a mixed-effects analysis of variance was run with group (3: Nap, Nap + Wake, Wake), valence (2: positive, negative), intentionality (2: incidental, intentional), and reward (2: rewarded, unrewarded) entered as factors of interest. This ANOVA yielded no significant interactions with valence (all $ps > .12$), and as such, positive and negative stimuli are grouped into one category (emotional) for all subsequent analyses. See Table 1 for a summary of memory performance separated by valence (negative, positive, neutral).

A mixed-effects analysis of variance was run on the corrected recognition rates (hits minus false alarms), with group (3: Nap, Nap + Wake, Wake), emotion (2: Emotional, Neutral), intentionality (2: Incidental, Intentional), and reward (2: Rewarded, Unrewarded) entered as factors of interest. This analysis determined

Table 1

Corrected Recognition Rates (Hits Minus False Alarms), Separated by Group, Valence, Intentionality, and Reward

<table>
<thead>
<tr>
<th></th>
<th>Nap</th>
<th>Nap + Wake</th>
<th>Wake</th>
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<tbody>
<tr>
<td></td>
<td>Neg</td>
<td>Pos</td>
<td>Neu</td>
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<tr>
<td>Intentionality</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Incidental</td>
<td>.50</td>
<td>.39</td>
<td>.27</td>
</tr>
<tr>
<td>Intentional</td>
<td>.53</td>
<td>.46</td>
<td>.40</td>
</tr>
<tr>
<td>Reward</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unrewarded</td>
<td>.46</td>
<td>.41</td>
<td>.32</td>
</tr>
<tr>
<td>Rewarded</td>
<td>.58</td>
<td>.44</td>
<td>.35</td>
</tr>
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that there was a main effect of group on corrected recognition, $F(2, 71) = 3.38, p < .08, \eta^2 = .087$, such that memory was enhanced when the delay included sleep (for the Nap and Nap + Wake groups) compared to when the delay did not include sleep.

There was a significant main effect of reward on corrected recognition, $F(1, 71) = 11.3, p < .001, \eta^2 = .14$, with rewarded stimuli better remembered than unrewarded stimuli (see Figure 1a). Although this did not interact with group, $F(2, 71) = .74, p = .48, \eta^2 = .02$, this effect of reward was significant in the Nap group ($p = .006$), marginally significant in the Nap + Wake group ($p = .054$), and not significant in the Wake group ($p = .344$).

There also was a significant main effect of emotion on corrected recognition, $F(1, 71) = 164.4, p < .001, \eta^2 = .70$ (see Figure 1b): Corrected recognition scores were greater for emotional items than neutral items, consistent with the emotional memory enhancement effect (see Buchanan & Adolphs, 2002, and Hamann, 2001, for reviews). The effect of emotion was significant within all three groups (all $p < .001$), and did not interact with group, $F(2, 71) = .21, p = .81, \eta^2 = .006$.

Further, there was a significant main effect of Intentionality on corrected recognition, $F(1, 71) = 23.1, p < .001, \eta^2 = .25$, with intentionally encoded stimuli better remembered than incidentally encoded stimuli (see Figure 1c). This effect of intentionality was qualified by a marginal Group $\times$ Intentionality interaction ($p = .058$), with post hoc $t$ tests determining that the effect of intentionality was significant within the groups that slept during the consolidation delay (Nap: $p = .001$; Nap + Wake: $p = .004$), but not within the Wake group ($p = .342$). There was suggestive evidence that this Group $\times$ Intentionality interaction was stronger for the neutral items than for the emotional items: There was a marginally significant three-way interaction between intentionality, emotion, and group ($p = .067$), and follow-up analyses confirmed that the Group $\times$ Intentionality interaction was significant only for the neutral items ($p = .022$) and not for the emotional items ($p = .24$; see Figure 1d).

**Discussion**

Replicating prior findings (e.g., Alger et al., 2010; Backhaus & Junghanns, 2006; Payne et al., 2015; Tucker et al., 2006), our data suggest that a consolidation interval consisting of a daytime nap enhances memory relative to an equivalent delay spent awake.
Inclusion of the Nap + Wake group allowed us to determine that these effects are not due to sleep simply protecting from interference (e.g., Wixted, 2004), but rather active consolidation (e.g., Ellenbogen, Payne, & Stickgold, 2006). The present study also substantiates prior literature showing that sleep does not consolidate all information equally, but rather has selective effects on memory for future-relevant information (e.g., Fischer & Born, 2009; Van Dongen et al., 2012; Wilhelm et al., 2011; see Stickgold, 2013 for review). For the first time, however, we focus on how sleep weights different cues for future relevance when these cues occur within the same stimuli. Particularly, these included cues of two different types: those related to bottom-up, stimuli-driven characteristics (emotion) and those related to top-down goals (reward, instructed learning).

First, we sought to answer whether there would continue to be beneficial effects of sleep for each of these cue types (e.g., Fischer & Born, 2009; Payne & Kensinger, 2011; Van Dongen et al., 2012), or if sleep would prioritize a certain cue (or cues) over others. Our results suggest that sleep prioritizes top-down, goal-directed cues (instructed learning, and to a lesser degree, reward) over bottom-up, stimulus-driven cues (emotion). Specifically, the Nap and Nap + Wake groups preferentially remembered the intentionally (vs. incidentally) encoded stimuli. The presence of a comparably significant effect in the Nap and Nap + Wake groups rules out an interference argument and suggests that sleep actively consolidates information that is instructed to be remembered. The Nap group also preferentially remembered rewarded (vs. unrewarded) stimuli, though because this effect was only of marginal significance in the Nap + Wake group, we cannot entirely rule out the possibility that a lack of interference partly contributed to the significant effect of reward in the Nap group.

One reason why the manipulation of instructed learning (i.e., whether participants incidentally encoded stimuli without knowledge of a later memory test vs. intentionally encoded stimuli for the purpose of a later memory test) was particularly successful in the present study may be because of the relatively short length of the consolidation delay. Prior work has found beneficial effects of sleep on to-be-tested information using overnight consolidation delays (e.g., Van Dongen et al., 2012; Wilhelm et al., 2011). Given that our results suggest that sleep hierarchically prioritizes information for consolidation, with cues related to top-down goals (i.e., instructed learning, reward) superseding those of bottom-up stimuli characteristics (i.e., emotion), the use of a short (2-hr) delay relative to a long (12-hr) delay perhaps amplified this prioritization. For instance, participants may have been more likely to believe that their efforts to remember information over two hours would successfully impact their performance, whereas memory after 12 hr may have seemed relatively outside their control.

In addition to determining whether sleep prioritizes certain cues, our second aim sought to test whether these cues for future relevance interact to influence memory consolidation. Results showed that beyond a preferential enhancement of sleep on memory for intentionally encoded stimuli, the magnitude of this enhancement depended on the emotionality of the stimuli. Particularly, a significant Group × Intentionality interaction was present only for neutral items (in which the only cue to future relevance was intentionality) and not emotional items (in which case both intentionality and emotion cued future relevance), suggesting that the effect of instructed learning is not additive above and beyond an emotional memory enhancement effect. In other words, when there are multiple cues for future relevance existing within the same stimuli, there may be diminishing returns beyond one cue; sleep may binarize information into whether it is future-relevant or not, strengthening memory based on category membership rather than based on the number of cues for future relevance. This is also consistent with a study by Baran, Daniels, and Spencer (2013), who instructed participants to memorize words that were each given a point value (i.e., testing an interaction of instructed learning and reward). They found that while participants showed greater memory following sleep, this did not depend on point value (Baran et al., 2013), providing additional support for the idea of subadditive interactions of future-relevant cues on memory: Once one cue for future relevance is present, there may be diminishing returns associated with the presence of additional cues. This also may explain why there was no selective effect of sleep on memory for emotional stimuli in the present study, as has been found in prior work (e.g., Hu et al., 2006; Payne et al., 2008; Wagner, Gais, & Born, 2001; Wagner, Hallschmid, Rasch, & Born, 2006). While this may initially seem surprising, it is important to take into account that prior studies did not incorporate other features of future relevance (instructed learning, reward). These data suggest that when multiple cues of prioritization exist within the same stimuli, sleep selects not the bottom-up cue of salience (emotion), but rather the top-down goal (instructed learning, and less so, reward) for preferential strengthening. The selective effects of sleep on emotional memory appear to be diminished when arguably stronger cues for future relevance, such as those related to top-down goals, are concurrently present.

In regards to the neural mechanisms underlying the selective consolidation of future-relevant information, it is possible that reactivation underlies both the consolidation of top-down goals and bottom-up cues to salience, as postulated by Oudiette and Paller (2013). However, if this is the case, the present study suggests that there may be a hierarchy in terms of what information is selectively consolidated, with instructed learning at the top of the ranks. Prior work using the targeted memory reactivation paradigm supports the idea that reactivation may preferentially strengthen information that is deemed future-relevant on the basis of instructed learning. For instance, within this paradigm, participants know that they are intentionally learning object-location associations for a future test. As such, in the present study, in which intentionally encoded information was better remembered than incidentally encoded information following sleep, it is likely that the to-be-remembered information was being preferentially reactivated during sleep, resulting in facilitated memory upon waking. While the present study does not investigate the contributions of specific sleep features to these selective benefits of sleep on memory consolidation, we speculate that preferential reactivation of intentionally encoded and rewarded objects in the hippocampus likely occurred during slow-wave sleep, as consistent with prior research (e.g., Antony, Gobel, O’Hare, Reber, & Paller, 2012; Lansink et al., 2009; Marshall & Born, 2007; Rasch, Bülch, Gais, & Born, 2007; Singer & Frank, 2009; Wilson & McNaughton, 1994).

It is possible that reactivation also underlies the selective consolidation of bottom-up, stimulus-driven characteristics during sleep. However, if this is the case, our results suggest that such cues to salience are prioritized to a lesser extent than intentionally...
encoded or rewarded information. There is also some evidence to suggest that in addition to reactivation, the preferential consolidation of emotional memories relies on other mechanisms. For example, using the targeted memory reactivation paradigm, Durrant, Power, and Lewis (2014) found that SWS duration and thalamocortical spindles led to faster memory judgments for negative, relative to neutral, picture-location associations that were reactivated during SWS, but found no benefit of reactivation to memory accuracy (Cairney, Durrant, Power, & Lewis, 2014). This is perhaps because reactivation has typically been described as a SWS mechanism, yet many believe that REM sleep may be more strongly associated with sleep-based emotional memory enhancements (e.g., Ackermann & Rasch, 2014; Nishida, Pearsall, Buckner, & Walker, 2009; Wagner, Gais, & Born, 2001; Walker, 2009, for review). It also has been suggested that certain features of REM sleep—theta oscillations that may enable enhanced connectivity between prefrontal regions and limbic regions, and high acetylcholine levels—may make REM sleep the ideal neurochemical environment for preferential consolidation of emotional information (see Bennion, Payne, et al., 2015, for review). Because the present study utilized a nap rather than an overnight consolidation interval, it is likely that some participants did not experience any REM sleep, or minimal REM sleep compared to a night spent asleep. Future work should assess how various factors (including top-down [e.g., goal-directed] and bottom-up [e.g., stimulus-driven] cues to salience) interact to influence memory utilizing an overnight consolidation period to elucidate what mechanisms may drive these findings, paying particular attention to the contribution of specific sleep stages and features to these selective benefits on memory consolidation.

Limitations

One limitation of the present work is that only self-report data were collected regarding participants’ sleep the night preceding the study; this retrospective report may be prone to inaccuracies. Even so, as participants reported obtaining at least 7 hr of sleep the 5 nights preceding the study, this minimizes the concern that differences in sleep debt affected the results. Further, including self-reported sleep duration the night before the study as a covariate did not influence the significance of the aforementioned results.

Another limitation is that naps had start times between noon and 2 p.m. While it would have been ideal for the nap to occur at exactly the same time for all participants, this was impossible due to participants’ class schedules and other scheduling conflicts. Also, there is a precedent for variation in daytime nap timing in investigating the effects of a nap on consolidation (e.g., Gorfine, Yeshurun, & Zisapel, 2007). Although these variations in nap start time may result in differences in sleep structure, because our results examine differences between groups who either did or did not sleep during the consolidation interval, these differences should only add variability to our data and should not be a confounding factor.

A potential concern for the Nap participants could be the effect of sleep inertia, the feeling of disorientation and performance impairment after waking. This feeling tends to be more severe when awakened from deep sleep (e.g., Rajaratnam & Arendt, 2001). Estimates on how long the effects of sleep inertia last widely vary, with some suggesting as little as 1 min (Webb & Agnew, 1964), less than 5 min (Naitoh, Kelly, & Bakkoff, 1993), 15–30 min (Dinges, Orne, & Orne, 1985; Groeger, Lo, Burns, & Dijk, 2011), to over 2 hr (Jewett et al., 1999). Importantly, only 9% of Nap + Wake participants (from whom we have PSG data) were awakened from deep sleep, with the majority of participants awakened from light sleep. This distribution minimizes concerns about sleep inertia. Moreover, the Nap + Wake participants had a 2-hr wake period after their nap prior to the recognition test, and the Nap group had an average of 12.5 ± 2.4 min between being awakened from their nap and the recognition test. These data suggest that it is unlikely that sleep inertia influenced the results, but regardless, because sleep inertia is known to impair performance, sleep inertia would not explain why the groups that slept during consolidation outperformed the Wake group in the present study.

Lastly, another limitation of the present study is that the Nap participants’ sleep was measured by actigraphy, as opposed to PSG. While PSG is viewed as the gold standard for sleep research, several studies have shown that the validity between actigraphy and PSG is relatively high in adult populations (e.g., 91%–93%; Sadeh, Sharkey, & Carskadon, 1994), with some supporting the use of actigraphy in lieu of PSG in healthy young adults such as those in this study (e.g., Ancoi-Itzrael et al., 2003; Kanady, Drummond, & Mednick, 2011). While we acknowledge that specificity (detection of wake) is generally low with actigraphy (e.g., 66% as measured during a daytime nap using the Motionlogger watch; Rupp & Balkin, 2011) and does not allow us to have precise information about the duration of sleep, average WASO was relatively low (i.e., ~11.1 min for the Nap group and ~6.8 min for the Nap + Wake group), suggesting that participants largely remained asleep once they fell asleep. As all Nap and Nap + Wake participants reported that they successfully slept, and the actigraphy data supported that self-report, this combination strongly suggests that all participants assigned to the nap conditions did sleep during the delay.

Conclusion

Overall, the present study addresses the important question of how sleep prioritizes information when multiple cues that signal prioritization exist within the same stimuli. Results suggest that sleep prioritizes information relevant to top-down goals rather than bottom-up characteristics of the stimuli, thus having important implications for education and vocational domains. In the present study, with participants having knowledge of a later memory test at the time of encoding, this research is particularly applicable to school settings, in which students are knowledgeable about the content that will be tested on an upcoming exam. The relevance to education, or any situation involving studying information for an upcoming test, is heightened when considering that the effects of instructed learning on memory following sleep were stronger for neutral information than emotional information; this suggests that telling individuals that information is going to be tested assigns salience to information that otherwise may not be particularly salient, leading to its preferential consolidation during a nap. While the mechanisms behind sleep’s preferential consolidation are still in need of further investigation, the present study leads us one step closer to understanding sleep’s selective effects on future-relevant information and perhaps toward utilizing manipulations of
future relevance that enable us to use sleep as a tool to enhance consolidation.

References


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