

# Memory, Sleep, and Dreaming: Experiencing Consolidation

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## KEYWORDS

- Sleep • Memory • Dreaming • Mentation • Cognition
- Consolidation • Default network • Resting states

During all stages of sleep, the mind and brain are working to process new memories, consolidating them into long-term storage and integrating recently acquired information with past experience. In recent years, an accumulating body of research evidence has definitively shown that postlearning sleep is beneficial for human memory performance across a variety of tasks, including verbal learning,<sup>1–4</sup> procedural skill learning,<sup>2,5–7</sup> emotional memory,<sup>8,9</sup> and spatial navigation.<sup>10,11</sup> Memories of recent experience appear nightly in the content of our dreams, and animal research shows that presleep experience is replayed on a cellular level during postlearning sleep. Sleep-dependent memory consolidation has been extensively examined from a variety of behavioral and neuroscientific perspectives, but studies examining dream experience as an indicator of mnemonic activity in the sleeping brain are conspicuously absent. This article reviews evidence that the use of subjective report as a method for probing the activities of the mind and brain is critical for a comprehensive approach to understanding memory consolidation. Recent work suggests that dream experiences recalled from sleep are a direct reflection of concomitant memory processes in the brain.

## MEMORIES IN THE SLEEPING BRAIN *The Reactivation and Consolidation of Memory during Sleep*

There is strong evidence that at least one function of sleep is to consolidate fragile new memory traces into more permanent forms of long-term storage, integrating key features of recent experience with existing remote and semantic memory networks. Behavioral studies in humans have clearly shown that postlearning sleep is beneficial for memory performance in a variety of learning domains. Until recently, much of this work focused on simple procedural tasks, showing that basic motor and perceptual skills were optimally developed across posttraining periods that included sleep, relative to equivalent periods of wakefulness. Accumulating data now also strongly implicate sleep in the consolidation of various forms of complex declarative memory, similarly showing that relative to wakefulness, sleep after learning leads to superior memory performance at later test.

Models of the brain processes supporting these mnemonic benefits of sleep have drawn heavily from animal literature showing a neural-level reactivation of recent experience during periods of posttraining sleep and quiet rest. Initially focusing on the hippocampus, this literature has now

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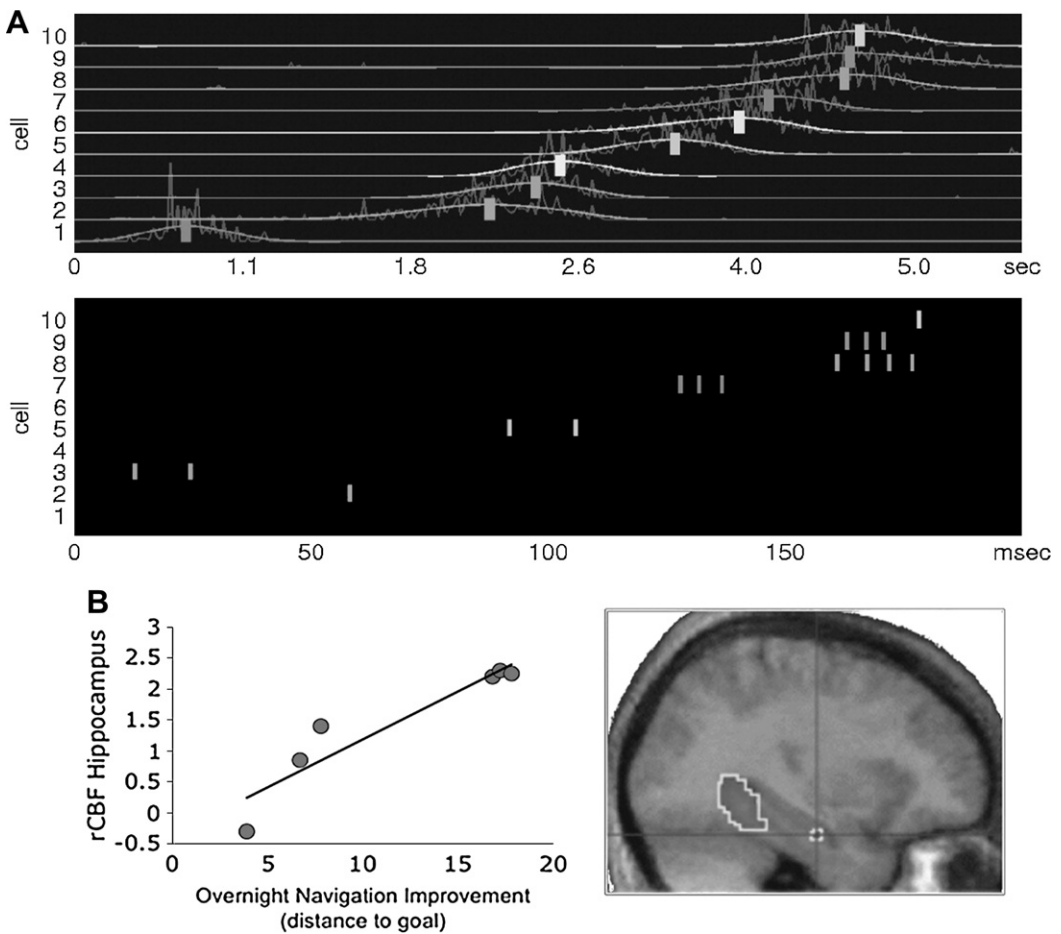
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shown that across a wide network of brain systems, patterns of neural activity that are first seen when waking animals are exploring an environment are later reproduced when these animals sleep. This reactivation has most consistently been observed during periods of nonrapid eye movement (NREM) sleep just after learning, during brief hippocampal sharp-wave ripple burst events<sup>12,13</sup> (Fig. 1A). This replay of memory in sleep may be critical to long-term memory consolidation. In direct support of this hypothesis, a recent study has shown that the extent of neural pattern reactivation after learning predicts subsequent gains in memory performance.<sup>14</sup> Human

neurophysiologic studies have linked consolidation to sleep-specific electrophysiologic and neurochemical events, and have used functional imaging technologies to show a systems-level reactivation of brain regions active in encoding new memories (Fig. 1B), roughly analogous to that which has been seen in rodents.

Classically, the consolidation of memory has been conceptualized as a process of strengthening an initially labile memory trace, such that the new memory is rendered increasingly resistant to interference across time. Much of the literature on sleep and memory has thus focused on simple quantitative measures of memory strength (eg, the



**Fig. 1.** (A) In animals, memory reactivation is seen as patterns of cell firings during waking exploration of an environment (*top*) that are reiterated in subsequent NREM sleep (*bottom*), albeit on a faster timescale. Vertical bars represent the time of peak firing for 10 individual cells, showing clear place fields in the training environment. (B) In humans, evidence of reactivation has been reported in imaging studies, showing that brain regions engaged during task encoding are again active during posttraining sleep. In this example, reactivation of hippocampal activity during posttraining sleep (*right*) predicted overnight improvement in memory performance on a spatial learning task (*left*). (Adapted from Lee AK, Wilson MA. Memory of sequential experience in the hippocampus during slow wave sleep. *Neuron* 2002;1186; with permission; and Peigneux P, Laureys S, Fuchs S, et al. Are spatial memories strengthened in the human hippocampus during slow wave sleep? *Neuron* 2004;541; with permission.)

number of words recalled, or the number of motor sequences completed). However, it is becoming clear that the role of sleep is more complex than strengthening memories in their original forms. To the contrary, recent studies have shown that sleep is important for such complex processes as the integration of new information into established cortical memory networks,<sup>15,16</sup> the extraction of meaning,<sup>17</sup> and the development of insight.<sup>18</sup> Recent studies by Dumay and Gaskell<sup>16</sup> and Tamminen and colleagues<sup>15</sup> describe the first of these concepts. As newly learned words become integrated into neocortical lexical networks over time, competition with previously known words develops, and this competition can be measured as slowed reaction times to those well-known words that are similar to the newly acquired words. In a lexical integration paradigm, participants learn a set of pseudowords that are phonemically similar to well-known words (eg, cathedruke is a pseudoword similar to the word cathedral) and response times to the new and old words are measured. Dumay and Gaskell<sup>16</sup> have reported that competition between new and existing words emerges only after a period of sleep, thus suggesting that newly learned words are integrated into neocortical lexical networks by sleep-dependent processes. Using the same task, Tamminen and colleagues<sup>15</sup> found that the degree of lexical integration over a night of sleep is associated with sleep spindles.

A recent study from our own laboratory suggests that sleep functions to transform memories such that the critical gist of an experience is retained, whereas specific details of the material are discarded. In the Deese-Roediger-McDermott paradigm, participants learn several lists of semantically related words. At a delayed test, when participants are asked to recall these words, often they also report having seen “gist” words, which describe the general theme of the memorized word lists, but which were not themselves present in the list. Sleep preferentially benefited (false) memory for these gist words, suggesting that one function of sleep-dependent memory processing is to extract meaningful generalities from large collections of related memories.<sup>17</sup> These and other recent studies suggest that sleep functions not simply to strengthen memories, but in addition to transform memory traces by integrating them into mnemonic networks and preferentially maintaining the general meaning or gist of the larger experience.

In parallel with this behavioral work, human brain imaging studies have described a sleep-dependent reorganization of the network of brain structures supporting subsequent recall.<sup>19–22</sup> For example, for hippocampus-dependent declarative

memories, retrieval-associated activity in the hippocampal complex decreases after sleep, whereas related activation in cortical structures, particularly medial prefrontal areas, increases.<sup>19,20</sup> Such evidence supports models of systems-level declarative memory consolidation proposing that memory retrieval, although initially dependent on the hippocampus for retrieval, becomes increasingly less reliant on the hippocampal system and more reliant on cortical structures over time,<sup>23</sup> and that this developing hippocampal independence may occur during sleep. Other functional magnetic resonance imaging (fMRI) studies have described an analogous sleep-dependent reorganization of emotional memory, such that medial prefrontal structures become more engaged at delayed retrieval when participants have been allowed to sleep immediately after encoding, in concert with increased retrieval-related functional connectivity between cortical and subcortical regions involved in emotional memory processing.<sup>21,22</sup> This type of functional memory reorganization, in which hippocampally dependent memories are gradually reencoded into cortical networks that rely on strongly overlapping and related representations, could underlie the ability of sleep to facilitate both the integration of recent memory with past experience and the abstraction of general concepts from specific stimulus material.

### ***Linking Sleep-dependent Memory Processing with Dream Experience***

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Given that humans dream, the neurophysiologic and fMRI evidence that memories are reactivated during sleep suggests that replay of experience in the sleeping brain could be related to the conscious experience of dreaming. Several key features of sleep-dependent memory reactivation and consolidation strongly parallel the form in which recently encoded memory appears in sleep mentation. These parallels are introduced in this section and expanded on in later sections.

First, qualitatively different types of memory seem to be processed preferentially during different stages of human sleep. Hippocampus-dependent memory, for example, seems to benefit particularly from NREM sleep, perhaps especially slow wave sleep (SWS), whereas memory for emotional material may be preferentially enhanced by rapid eye movement (REM) sleep. Mirroring these proposed mnemonic functions of REM and NREM sleep, characteristics of dream experience vary similarly as a function of sleep stage. For example, subjective reports elicited from NREM sleep stages are more likely to contain episodic

memory sources (a hippocampus-dependent form of memory) than are reports from REM sleep,<sup>24</sup> whereas dream experiences from REM sleep are unique in the presence of particularly intense emotions.<sup>25</sup>

Second, a prominent feature of memory reactivation in rodent models is that, within NREM sleep, the strength of neural-level memory replay decays quickly across time.<sup>26,27</sup> Similarly, it seems that sleep mentation may be most strongly related to recent memories early in the sleep phase,<sup>24,28,29</sup> with this association to recent experience decreasing over time.

Earlier, we also introduced the concept that sleep transforms human memories, rather than veridically strengthening them. Both rodent neural reactivation studies and data on human dreaming support this notion that recent experience is not faithfully replayed in videotape-like fashion during sleep. Neuronal firing sequences established during wake are reexpressed only intermittently during rodent NREM sleep, with low fidelity and on a faster timescale than the original experience.<sup>30,31</sup> Similarly, only intermittent fragments of recent episodic memories appear in sleep mentation, intermingled with remote and semantically related material.<sup>29,32</sup>

Third, there are several key features of the organization of the sleeping brain believed to play a critical role in supporting both offline memory processing and the formation of dream experience. As we fall asleep, the brain quickly undergoes dramatic changes in functional activation patterns, and in the composition of the neurochemical/neurohormone milieu driving the system. During all stages of sleep, regional cerebral blood flow to a network of frontal areas is dramatically decreased, relative to waking,<sup>33</sup> whereas activity in a network of memory-related areas, including the hippocampal complex, medial prefrontal cortex, and anterior cingulate, remains relatively increased during both REM and NREM sleep stages. As we enter early-night NREM-dominated sleep, levels of acetylcholine are dramatically reduced relative to waking, so that monoaminergic neurotransmitters dominate the system. These low levels of acetylcholine during NREM sleep have been hypothesized to facilitate the offline consolidation of hippocampus-dependent memory,<sup>34</sup> during a time at which recent episodic memories are most likely to be appearing in concomitant dream experience.<sup>24,29</sup> Reduced levels of cortisol during early night, SWS-dominated sleep have also been hypothesized to both facilitate hippocampal-cortical interactions underlying memory consolidation<sup>35,36</sup> and to promote brain dynamics supporting NREM-type dream experience.<sup>36</sup>

Recent papers in sleep and memory have liberally speculated on a possible connection between sleep-dependent memory processing on the one hand, and the imagery, thoughts, and feelings comprising dream experience on the other.<sup>30,36-40</sup> Most recently, observations that the replay of memory in sleeping rodents occurs not only in the hippocampus but in sensory cortices as well have seemed to offer empirical evidence that “the expression of these reactivated memory traces in sensory cortex may directly relate to the perceptual imagery experienced during sleep and dream states.”<sup>30</sup> However, the presence of memory-related brain activity during sleep does not necessarily imply that this activity is consciously experienced, and hence does not imply a relationship to dream experiences recalled from this period of sleep. Until recently, little empirical work has attempted to directly test the hypothesis that dream experience reflects the reactivation and consolidation of specific mnemonic content in the sleeping brain. Before describing these studies, we consider the nature of incorporation of recent experiences into sleep mentation more generally, and describe how these observations can inform our approach to understanding offline memory consolidation processes.

## THE INCORPORATION OF RECENT EXPERIENCE INTO DREAMING

Recent memories constitute a significant component of sleep mentation. In 1900, Freud<sup>41</sup> coined the term “day residue” to describe the presence of recent life experience in dream content, a phenomenon which he viewed as only secondary in relevance to the true latent meaning of a dream. But as the notion that dreams harbor a secret meaning decipherable only by trained psychoanalysts has fallen into disfavor, it has become increasingly clear that the appearance of newly encoded information in our daydreams, mental imagery, thoughts, and dreams may be an observation of paramount importance to understanding the activities of mind and brain during both wake and sleep. The form in which memories are incorporated into dream experience in many ways parallels what we know about memory consolidation during sleep, and may help us to understand the process of long-term memory consolidation.

### *Effects of Presleep Experience on Sleep Mentation*

In the 1960s and 1970s, a considerable amount of research effort was devoted to understanding the relation of waking events to dream content by manipulating participants' presleep experience.

Despite methodological weaknesses that plagued much of this literature, several useful conclusions can be drawn from this early work. Most notable is the extreme difficulty of manipulating dream content, even when highly emotional stimuli are introduced before sleep. Of the dozens of such studies performed during this time,<sup>42–47</sup> almost none showed unambiguous, statistically significant effects of an experimentally introduced presleep stimulus on subsequent dream content. The most consistently observed effect of waking experience on laboratory-collected sleep mentation has been a powerful influence of the laboratory setting itself. For example, in an analysis of 813 REM mentation reports collected across several studies, Dement and colleagues<sup>48</sup> reported that 22% of reports unambiguously incorporated either isolated elements of the laboratory situation (eg, the experimenter, electrodes) or more complete representations of the experimental setting (ie, a combination of these elements). In retrospect, given the salience of sleeping in a strange place and being awakened during the night to report dreams, it is hardly surprising that the laboratory environment overshadows the effect of any particular film or activity introduced as part of an experimental protocol. In contrast, more recent data from our own laboratory, discussed later, show that experimental introduction of intensive and engaging learning experiences can dramatically influence the content of dreaming, at least early in the night.

Other, nonexperimental approaches provide solid empirical evidence that the content of sleep mentation often references new memories and recent experiences. For example, in an analysis comparing 299 home-collected dream reports with possible memory sources from a diary of waking events, Fosse and colleagues<sup>32</sup> reported that fragments of recent experience are often seen in dreams. Although exact replication of any particular waking experience was rare, 51% of reports were judged to contain at least one dream element bearing strong similarity to a recent waking experience. Other research has similarly prompted participants to connect dream reports with likely memory sources from waking experience in the previous days and weeks,<sup>24,49–51</sup> showing that such memory sources are readily identified with high confidence, and correspond with the ratings of blind judges.<sup>49</sup> We return later to this notion that recent experience appears in sleep mentation in a fragmentary form, rather than as an exact videotape-like replay of an event.

Other lines of work have explored the more general correspondence between sleep mentation and waking life. In collaboration with Robert Van

de Castle, Calvin Hall<sup>52</sup> pioneered the use of content analysis methods to quantitatively assess the content of large sets of mentation reports. A response to the methodological pitfalls inherent in subjective interpretations of dream content used by psychoanalysts, this meticulous classification system counts the occurrence of different types of characters, settings, objects, social interactions, activities, and so forth, explicitly described in the text of mentation reports. Using this system, Hall illustrated the transparent relationship between dream content and everyday life by creating surprisingly accurate profiles and histories of psychiatric patients based solely on blind content analysis of dream reports, and became amongst the first to champion the notion that quantitative methods could uncover straightforward and meaningful relationships between waking experience and dream content.

“A large number of dreams reflect faithfully the daytime activities and preoccupations of the dreamer. Skiers dream of skiing, surfers dream of surfing, and mountain climbers dream of climbing mountains. Teachers dream of classroom situations, bankers dream of banking activities, and nurses dream about their patients.”<sup>53</sup>

More recent applications of Hall’s system of content analysis have reported consistent, statistically significant differences in dream content of groups of individuals with divergent waking experience (ie, between males and females, children and adults, blind and sighted individuals [for a review, see Ref.<sup>54</sup>]). These investigations have contributed to our understanding of the dreaming process by reminding us that, although attempts to predict or control dream content have often failed, a broad correspondence between sleep mentation and waking experience is nonetheless transparently obvious.

### ***Determinants of the Memory Sources of Dreaming***

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But what determines which memories contribute to the content of dreaming on a particular night? Far from being a haphazard process, the incorporation of waking experience into sleep mentation seems to follow a set of predictable patterns, modulated by both sleep stage and temporal distance from a waking event. Contrary to the entrenched popular belief that REM sleep = dreaming, we dream during all stages of sleep.<sup>55–58</sup> Although reports of mental experiences from NREM sleep stages 2, 3, and 4 are often shorter and less emotional than REM reports, there is considerable overlap in the cognitive characteristics of reports from different stages of sleep

(eg, see Ref.<sup>59</sup>). Late-night NREM dreaming can be just as vivid, bizarre, and storylike as the typical dream from REM sleep.<sup>57,60</sup> Yet one consistent difference between dream reports from different stages of sleep seems to be the nature of participant-identified memory sources. Coinciding with the notion that NREM dreams tend to be more realistic and mundane than reports from REM sleep, mentation reports from NREM stages are characterized by a large proportion of episodic memory sources,<sup>24</sup> derived from memories of specific autobiographical events that occurred at a particular place and time. Dream reports from REM sleep, on the other hand, incorporate more abstract and semantic memory sources, unrelated to specific life events. Thus, during NREM sleep a participant might report a dream concerning a friend she saw the previous afternoon, whereas dreams during later REM sleep would likely be more bizarre and not obviously connected to any specific presleep experience.

The incorporation of recent experience into dream content also seems to follow an organized temporal pattern. Very recent events are more often incorporated into mentation occurring early in the sleep phase, with remote experiences appearing only later in the night. Although only a few studies have examined time-of-night effects on incorporation in this manner, both the recency of subject-identified memory sources<sup>61</sup> and the similarity of sleep mentation reports to presleep thought<sup>62</sup> have been reported to correlate negatively with time since sleep onset. Work from our own laboratory using engaging video game learning tasks has shown that incidence of direct, unambiguous incorporation of task-related imagery at sleep onset declines linearly as a function of time since the initiation of sleep.<sup>28,29</sup> On a broader timescale, it seems that recent life events are most likely to appear in dream content, relative to more remote experiences from years past.<sup>63,64</sup> Several studies also suggest that waking experiences tend to be incorporated into dream mentation either immediately after the experience, or else about a week later (the dream lag effect<sup>49,65</sup>).

These observations lead us to conclude that NREM sleep early in the night is the state of sleep most likely to contain replay of recent memory. As described earlier, this notion is supported by the animal literature, in which neuronal-level memory reactivation has typically been observed during periods of NREM sleep immediately after learning, with the strength of this replay decaying rapidly across time. In contrast, only a single study has reported similar reactivation of memory during REM sleep.<sup>39</sup> Our recent work examining the effects of

learning tasks on sleep mentation have thus focused on periods of stage 1 and 2 NREM sleep immediately after sleep onset.

### ***The Effects of Intensive Learning Experiences on Sleep Onset Mentation***

Studies in our own laboratory have examined NREM sleep mentation after intensive training on engaging, video-gamelike tasks. Concentrating on periods of early night NREM sleep, this research shows that salient, interactive learning tasks can exert a dramatic influence on subsequent sleep mentation. In one such study, participants played the video game Tetris extensively several hours before sleep.<sup>28</sup> When mentation reports were then repeatedly elicited after short intervals of sleep, 64% of participants reported unambiguous game-related images in at least one sleep onset report. In a related investigation using a downhill skiing arcade game,<sup>29</sup> 30% of all posttraining mentation reports directly incorporated the game (**Fig. 2**). The frequency of direct incorporation in these sleep onset studies, dramatically higher than that observed in any previous overnight investigation, suggests that the first minutes of sleep provide ideal conditions for the cognitive-level reactivation of waking experience. Furthermore, it may be that interactive learning experiences are more likely to be reactivated as participants fall asleep than are passively viewed experimental stimuli.

### ***Interleaved Fragments of Experience***

Despite the strong influence of waking experience on subsequent sleep mentation, dreams rarely consist of an exact replay of a life event. Instead, sleep mentation incorporates isolated elements of a waking episode, intermingled with fragments of other recent memories, as well as remote and semantic memory material, thus creating novel and sometimes bizarre scenarios that do not faithfully represent any particular waking event. For example, the following illustrates a sleep onset dream report that clearly incorporates fragments of a waking experience, but without replicating the original context in which these fragments were embedded (data from Ref.<sup>32</sup>).

#### ***Waking experience***

*When I left [work at] Starbucks, we had so many leftover pastries and muffins to throw away or take home, I couldn't decide which muffins to take and which to toss ...*



**Fig. 2.** After training on an engaging downhill skiing arcade game, 30% of 386 sleep onset mentation reports contained task-related imagery or thoughts. Representation of the game primarily took the form of sensory imagery as opposed to thought, and most often bore a direct, unambiguous relationship to the game. Examples of direct incorporation: "I get like flashes of that ... game in my head, virtual reality skiing game ... downhill umm race, in my head. Umm, there's this one particular corner that I haven't quite been able to master, and every time I get flashes of it, it's like that corner that umm I keep crashing into in my head." "I once again, saw the, the game, it was smooth at first, and then it went into the cave, and then it just stopped like abruptly, like the game turned off." Examples of indirect incorporation: "I was picturing stacking wood this time ... I felt like I was doing it at ... at a ski resort that I had been to before, like 5 years ago maybe." "I was in a race. Um, like a running race, um ... sort of like through San Francisco. It was kind of hilly and it wasn't difficult. Like, I was just kind of coasting through the race I think." (*Adapted from Wamsley EJ, Perry K, Djonlagic I, et al. Cognitive replay of visuo-motor learning at sleep onset: temporal dynamics and relationship to task performance. Sleep 2010;33:59; with permission.*)

### Corresponding sleep mentation

*My dad and I leave to go shopping. We go from room to room, store to store. One of the stores is filled with muffins, muffins, muffins from floor to ceiling, all different kinds, I can't decide which one I want ...*

In studies of sleep onset and stage 2 NREM sleep reports after playing video games,<sup>28,29</sup> we have similarly observed that, rather than faithfully reiterating a learning task, mentation reports integrated elements of the learning experience into a narrative that included related material drawn from remote and semantic memory. For example, after training on a downhill skiing arcade game,<sup>29</sup> one participant reported at sleep onset, "I was picturing stacking wood this time ... I felt like I

was doing it at ... at a ski resort that I had been to before, like 5 years ago maybe.." Similarly, after training on a virtual maze navigation task,<sup>66</sup> a participant reported "I was thinking about the maze and kinda having people as check points, I guess, and then that led me to think about when I went on this trip a few years ago and we went to see these bat caves, and they're kind of like, mazelike." Thus, when incorporated into a dream, the various components of a wake episode do not seem to remain bound together in the way that characterizes the mental time travel of episodic memory recall in waking life.

This observation that dreams do not veridically replay waking experience has led some to conclude that such mental activity is incompatible with consolidation of memory.<sup>67,68</sup> To the contrary, emerging evidence suggests that the fragmentary form in which waking experience appears in dreams, intermingled with other memory traces, reflects a critical feature of the memory consolidation process. As described earlier, consolidation seems to be considerably more complex than the strengthening of memories in their original forms, and the neuronal-level memory reactivation described in animals does not consist of a precise, veridical reiteration of waking experience. Instead, patterns of neural activity that statistically resemble (but are not identical to) those established in waking experience are played out on a speeded timescale. Furthermore, when animals are exposed to 2 successive spatial experiences, reactivation of both patterns seems to be instantiated simultaneously during subsequent NREM sleep.<sup>26</sup> Compatible with this observation is the proposal that sleep functions to transform memory traces in part by slowly interleaving neural representations of recent experience into existing remote and semantic cortical networks.<sup>38,69</sup> For example, in their influential article in *Psychological Review*, McClelland and colleagues speculate that optimal consolidation of new memories requires the alternating reactivation of these memories and related remote memories during different stages of sleep:

*Once a memory is stored in the hippocampal system, it can be reactivated and then reinstated in the neocortex ... [R]einstatement provides the opportunity for an incremental adjustment of neocortical connections, thereby allowing memories initially dependent on the hippocampal system to gradually become independent of it. We assume that reinstatement also occurs in off-line situations, including active rehearsal, reminiscence, and other inactive states including*

*sleep ... Possibly, events reactivated in the hippocampus during slow wave sleep prime related neocortical patterns, so that these in turn become available for activation during REM sleep. This could permit both new and old information to be played back in closely interleaved fashion.*<sup>69</sup>

Following this line of reasoning, we propose that even within a single dream experience, sleep mentation reflects the interleaved reactivation of memory fragments from different recent and remote sources, allowing newly acquired information to become increasingly connected with related memory traces across time. By initiating long-term potentiation-like plasticity in mnemonic networks, this simple process of simultaneously activating new and old memory traces during sleep could account for behavioral data indicating that sleep facilitates the integration of new information with existing semantic networks,<sup>15,16</sup> as well as the extraction of meaning,<sup>17</sup> which may require a similar process of relating new information to existing knowledge. However, despite many hypotheses relating the conscious experience of dreaming to memory processing, this notion is yet to be subjected to systematic empirical investigation.

### THE EMPIRICAL STUDY OF SPONTANEOUS SUBJECTIVE EXPERIENCE

For the most part, cognitive neuroscience has abandoned the behaviorist notion that conscious, subjective experience is not a suitable object for empirical investigation. Research in the last 2 decades has moved beyond the philosophic question of mind-brain relationship and begun in earnest to study the neural correlates, for example, of motivation, emotion, attention, mental imagery, and episodic memory. Often, mapping the brain basis of these subjective concepts relies on taking participants' verbal reports of experience at face value. Yet neuroscience has been slow to formalize the study of spontaneous subjective experience during offline states, when responses to sensory stimuli no longer drive the system. Although research on the default mode of brain function has brought attention to the importance of spontaneous brain activity occurring during periods of rest and sleep,<sup>70,71</sup> virtually none of this work has examined participants' own reports of what is going through their mind at rest. Data on spontaneous cognition during sleep have been even more lacking. Neurophysiologic studies seeking to shed light on the neural basis of dreaming have often relied merely on describing

the physiology of REM, or else have dichotomized conscious experience as either present or absent, without exploring the content of this mentation.

Earlier, we argued that the specific content of conscious experience during sleep (whether termed sleep mentation, dreaming, or hypnagogic imagery) is clearly relevant to understanding memory consolidation. Yet despite widespread theoretic agreement that sleep-dependent memory processing may relate to dream experience,<sup>30,36–40,72</sup> attempts to empirically address this hypothesis have been conspicuously absent. Why? First, for historical reasons, dream experience has typically been presumed to be difficult or impossible to quantify in a scientifically rigorous manner. Psychoanalytic approaches entrenched in the popular imagination have characterized dreaming as a mysterious, symbolic form of mental activity that, unlike waking cognition, cannot be measured, classified, and quantitatively analyzed in a meaningful way. Pseudoscientific approaches to dreaming popularized in the media have created a perception that, when occurring during sleep, cognition is not a legitimate area of scientific inquiry. This is not the case. There is little, if any, evidence that conscious experience during sleep is particularly more inaccessible, complex, or symbolic than waking thought. Furthermore, reliable approaches to quantifying dream content have been available for decades,<sup>52,59</sup> and methods of data collection are straightforward and completely compatible with standard designs in memory research. Although memory for sleep mentation is typically more fleeting than for waking experience, all self-report measures, whether for waking or sleep mentation, rely on taking post hoc reports of unverifiable data at face value ("Did you see the stimulus?" "What strategy did you use to encode the material?" "To what degree have the following symptoms bothered you in the past month?"). Resurgent studies of such subjective concepts as emotion, mood, memory, and belief show the progress that can be made when one takes a simple and straightforward approach to subjective experience, casting obfuscating philosophic concerns aside.

Critically, the content of spontaneous subjective experience can provide information inaccessible via any other means. The use of subjective report is an ideal method to determine whether a specific memory is being reactivated in the sleeping brain. Particularly in human research, there is no known measure of brain activity (eg, electroencephalography, fMRI, positron emission tomography) that can convincingly show the activation of a specific memory. For example, increased regional cerebral blood flow to learning-related brain regions



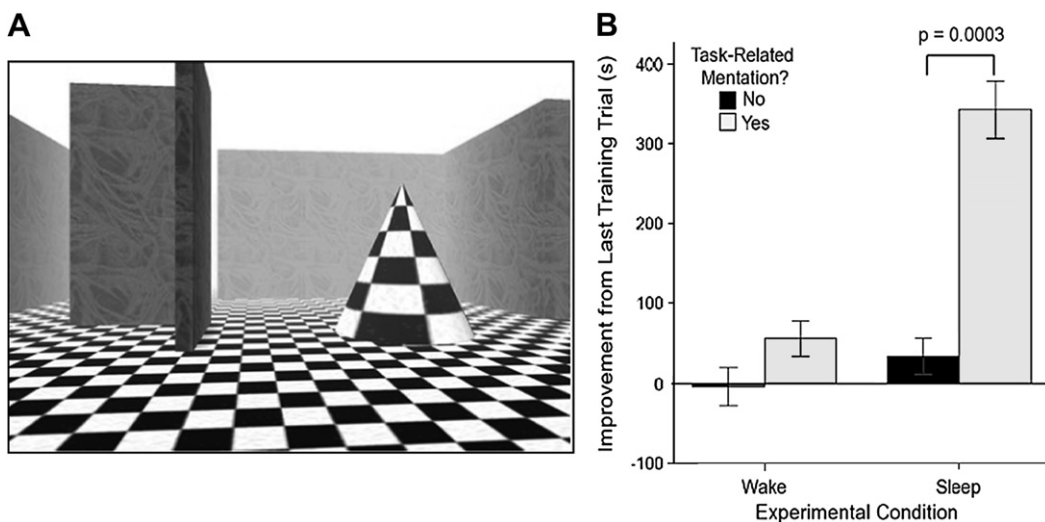
suggests that the same memory systems engaged at learning are doing something during sleep, but does not show the reactivation of a particular memory. Conscious retrieval of a recent memory, in contrast, definitely shows that the neural networks encoding that particular memory have been reactivated. Subjective reports allow us a detailed view of the form in which a memory is retrieved. For example, as described earlier, reports of sleep mentation reveal that recent memory fragments are reactivated in an interleaved fashion with past experience and semantic knowledge. Such observations illuminate how the brain transforms memories over time by integrating recently acquired information into existing knowledge structures. Reports of conscious experience are unique in enabling us to explore which memories of everyday waking experience are spontaneously reactivated during offline states of quiet rest and sleep.

### REACTIVATION OF MEMORY IN DREAM CONTENT AND SLEEP-DEPENDENT MEMORY CONSOLIDATION

Although empirical investigation of these questions has been largely lacking, a handful of studies provide noteworthy evidence for a link between learning, sleep-dependent memory consolidation, and dream experience. That dreaming might function to process previous experience is a hypothesis predating the current resurgence of interest in sleep-dependent memory consolidation, and several studies from the 1960s onwards have

addressed this question. Fiss and colleagues<sup>73</sup> investigated the morning recall of short stories encoded the night before, finding a correlation between story-related words in dream reports and memory for these stories the following morning. De Koninck and colleagues<sup>74,75</sup> have also examined the correlation between sleep mentation and verbal learning, exploring dream content as a corollary of language learning in an academic setting. Amongst students enrolled in a French-immersion language class, those who showed superior acquisition of the new language across a 6-week course tended to incorporate French into dream content more often than students who were less successful in the class.<sup>74,75</sup> Hypothesizing that REM sleep dreaming is important for emotional adaptation to stressful events, the work of Rosalind Cartwright has examined dream content as a predictor of psychological outcomes in women after divorce, finding that characteristics of spouse-related dreams predict remission from depression.<sup>76</sup> Other work also supports a role for sleep in emotional adaptation to negative experiences.<sup>77,78</sup>

Recent work from our own laboratory has provided direct evidence that incorporation of a learning task into subsequent dream experience predicts enhanced sleep-dependent memory consolidation.<sup>66</sup> In this study, participants were trained on a three-dimensional style virtual maze task (Fig. 3, left) before an opportunity for a 1.5-hour nap or else for an equivalent period of wake. During this period, all subjects were



**Fig. 3.** (A, B) Dreaming of a spatial learning task is associated with enhanced navigation performance at delayed retest, whereas thinking of the task during wakefulness is unrelated to later performance. Error bars represent  $\pm$  standard error of the mean. (Adapted from Wamsley EJ, Tucker M, Payne JD, et al. Dreaming of a learning task is associated with enhanced sleep-dependent memory consolidation. *Curr Biol* 2010;20:850; with permission.)

prompted 3 times to make open-ended verbal reports of “everything that was going through your mind.” We found that reports of task-related mentation were strongly associated with enhanced performance at subsequent retest (Fig. 3, right). In the sleep group, participants who spontaneously referred to the maze task in their subjective reports improved 10-fold more at retest than sleep participants who gave no task-related reports ( $P = .0003$ ). In contrast, thinking of the maze while awake did not provide any performance benefit (condition  $\times$  mentation interaction:  $P = .08$ ). These findings show how reports of subjective experience can inform the study of memory consolidation, providing novel evidence that dream experience reflects the learning-induced reactivation of memory networks during sleep, and that such reactivation correlates with substantially enhanced memory performance.

## SUMMARY

Recent advances in our understanding of long-term memory processing suggest that after learning, waking experience is reactivated in the sleeping brain, leading to a process of consolidation by which new, labile memory traces are reorganized into more permanent forms of long-term storage. Dream experiences recalled from sleep bear a transparent relationship to recently encoded information, and provide a useful window into consolidation-related activities of the sleeping brain. Recent work from our laboratory has established a direct relationship between the replay of recent experience in dream content, and enhanced memory performance in humans.<sup>66</sup>

We have argued here that the study of spontaneous conscious experience has great potential for elucidating the mechanisms of offline memory processing, particularly by allowing an examination of precisely which memories from everyday experience are reactivated during offline states, and by providing detailed information on the activities of memory systems that is not available by any other means. It is our hope that future research will profitably focus on the quantification of subject experience during periods of quiet rest and sleep, relating neural and behavioral measures of memory consolidation to the particular form in which new information is incorporated into dreaming, interleaved with established remote and semantic memory networks.

## REFERENCES

1. Ellenbogen JM, Hulbert JC, Stickgold R, et al. Interfering with theories of sleep and memory: sleep, declarative memory, and associative interference. *Curr Biol* 2006;16:1290.
2. Plihal W, Born J. Effects of early and late nocturnal sleep on declarative and procedural memory. *J Cogn Neurosci* 1997;9:534.
3. Tucker MA, Hirota Y, Wamsley EJ, et al. A daytime nap containing solely non-REM sleep enhances declarative but not procedural memory. *Neurobiol Learn Mem* 2006;86:241.
4. Schabus M, Gruber G, Parapatics S, et al. Sleep spindles and their significance for declarative memory consolidation. *Sleep* 2004;27:1479.
5. Stickgold R, Whidbee D, Schirmer B, et al. Visual discrimination task improvement: a multi-step process occurring during sleep. *J Cogn Neurosci* 2000;12:246.
6. Walker MP, Brakefield T, Morgan A, et al. Practice with sleep makes perfect: sleep-dependent motor skill learning. *Neuron* 2002;35:205.
7. Huber R, Ghilardi MF, Massimini M, et al. Local sleep and learning. *Nature* 2004;430:78.
8. Wagner U, Gais S, Born J. Emotional memory formation is enhanced across sleep intervals with high amounts of rapid eye movement sleep. *Learn Mem* 2001;8:112.
9. Nishida M, Pearsall J, Buckner RL, et al. REM sleep, prefrontal theta, and the consolidation of human emotional memory. *Cerebral Cortex* 2009;19:1158.
10. Peigneux P, Laureys S, Fuchs S, et al. Are spatial memories strengthened in the human hippocampus during slow wave sleep? *Neuron* 2004;44:535.
11. Wamsley EJ, Tucker MA, Payne JD, et al. A brief nap is beneficial for human route-learning: the role of navigation experience and EEG spectral power. *Learn Mem* 2010;17:332.
12. Buzsaki G. Memory consolidation during sleep: a neurophysiological perspective. *J Sleep Res* 1998;7(Suppl 1):17.
13. Buzsaki G. Hippocampal sharp waves: their origin and significance. *Brain Res* 1986;398:242.
14. Dupret D, O'Neill J, Pleydell-Bouverie B, et al. The reorganization and reactivation of hippocampal maps predict spatial memory performance. *Nat Neurosci* 2010;13:995.
15. Tamminen J, Payne JD, Stickgold R, et al. Sleep spindle activity is associated with the integration of new memories and existing knowledge. *J Neurosci* 2010;30(43):14356–60.
16. Dumay N, Gaskell MG. Sleep-associated changes in the mental representation of spoken words. *Psychol Sci* 2007;18:35.
17. Payne JD, Schacter DL, Propper RE, et al. The role of sleep in false memory formation. *Neurobiol Learn Mem* 2009;92:327.
18. Wagner U, Gais S, Haider H, et al. Sleep inspires insight. *Nature* 2004;427:352.
19. Takashima A, Nieuwenhuis IL, Jensen O, et al. Shift from hippocampal to neocortical centered retrieval

- network with consolidation. *J Neurosci* 2009;29:10087.
20. Takashima A, Petersson KM, Rutters F, et al. Declarative memory consolidation in humans: a prospective functional magnetic resonance imaging study. *Proc Natl Acad Sci U S A* 2006;103:756.
  21. Payne JD, Kensinger EA. Sleep leads to changes in the emotional memory trace: evidence from fMRI. *J Cogn Neurosci* 2010. [Epub ahead of print]. DOI:10.1162/jocn.2010.21526.
  22. Sterpenich V, Albouy G, Darsaud A, et al. Sleep promotes the neural reorganization of remote emotional memory. *J Neurosci* 2009;29:5143.
  23. Frankland PW, Bontempi B. The organization of recent and remote memories. *Nat Rev Neurosci* 2005;6:119.
  24. Baylor GW, Cavallero C. Memory sources associated with REM and NREM dream reports throughout the night: a new look at the data. *Sleep* 2001;24:165.
  25. Smith MR, Antrobus JS, Gordon E, et al. Motivation and affect in REM sleep and the mentation reporting process. *Conscious Cogn* 2004;13:501.
  26. Kudrimoti HS, Barnes CA, McNaughton BL. Reactivation of hippocampal cell assemblies: effects of behavioral state, experience, and EEG dynamics. *J Neurosci* 1999;19:4090.
  27. Wilson MA, McNaughton BL. Reactivation of hippocampal ensemble memories during sleep. *Science* 1994;265:676.
  28. Stickgold R, Malia A, Maguire D, et al. Replaying the game: hypnagogic images in normals and amnesics. *Science* 2000;290:350.
  29. Wamsley EJ, Perry K, Djonlagic I, et al. Cognitive replay of visuomotor learning at sleep onset: temporal dynamics and relationship to task performance. *Sleep* 2010;33:59.
  30. Ji D, Wilson MA. Coordinated memory replay in the visual cortex and hippocampus during sleep. *Nat Neurosci* 2007;10:100.
  31. Nadasdy Z, Hirase H, Czurko A, et al. Replay and time compression of recurring spike sequences in the hippocampus. *J Neurosci* 1999;19:9497.
  32. Fosse MJ, Fosse R, Hobson JA, et al. Dreaming and episodic memory: a functional dissociation? *J Cogn Neurosci* 2003;15:1.
  33. Braun AR, Balkin TJ, Wesenten NJ, et al. Regional cerebral blood flow throughout the sleep-wake cycle. An H2(15)O PET study. *Brain* 1997;120:1173.
  34. Hasselmo ME. Neuromodulation: acetylcholine and memory consolidation. *Trends Cogn Sci* 1999;3:351.
  35. Plihal W, Born J. Memory consolidation in human sleep depends on inhibition of glucocorticoid release. *Neuroreport* 1999;10:2741.
  36. Payne JD, Nadel L. Sleep, dreams, and memory consolidation: the role of the stress hormone cortisol. *Learn Mem* 2004;11:671.
  37. Cai DJ, Mednick SA, Harrison EM, et al. REM, not incubation, improves creativity by priming associative networks. *Proc Natl Acad Sci U S A* 2009;106:10130.
  38. Paller KA, Voss JL. Memory reactivation and consolidation during sleep. *Learn Mem* 2004;11:664.
  39. Louie K, Wilson MA. Temporally structured replay of awake hippocampal ensemble activity during rapid eye movement sleep. *Neuron* 2001;29:145.
  40. Walker MP, van der Helm E. Overnight therapy? The role of sleep in emotional brain processing. *Psychol Bull* 2009;135:731.
  41. Freud S. *The interpretation of dreams*. New York: Random House; 1900.
  42. Cartwright R. *The relation of daytime events to the dreams that follow*. In: Hartmann E, editor. *Sleep and dreaming*. Boston: Little, Brown and Company; 1970. p. 227.
  43. Baekeland F. *Laboratory studies of effects of presleep events on sleep and dreams*. *Int Psychiatry Clin* 1970;7:49.
  44. Breger L, Hunter I, Lane RW. *The effect of stress on dreams*, vol. 7. New York: International Universities Press; 1971.
  45. Foulkes D, Rechtschaffen A. *Presleep determinants of dream content: effect of two films*. *Percept Mot Skills* 1964;19:983.
  46. Goodenough DR, Witkin HA, Koulack D, et al. The effects of stress films on dream affect and on respiration and eye-movement activity during Rapid-Eye-Movement sleep. *Psychophysiology* 1975;12:313.
  47. Witkin HA, Lewis HB. *The relation of experimentally induced presleep experiences to dreams. A report on method and preliminary findings*. *J Am Psychoanal Assoc* 1965;13:819.
  48. Dement WC, Kahn E, Roffwarg HP. *The influence of the laboratory situation on the dreams of the experimental subject*. *J Nerv Ment Dis* 1965;140:119.
  49. Nielsen TA, Kuiken D, Alain G, et al. *Immediate and delayed incorporations of events into dreams: further replication and implications for dream function*. *J Sleep Res* 2004;13:327.
  50. Cavallero C. *Dream sources, associative mechanisms, and temporal dimension*. *Sleep* 1987;10:78.
  51. Cavallero C, Foulkes D, Hollifield M, et al. *Memory sources of REM and NREM dreams*. *Sleep* 1990;13:449.
  52. Hall C, Van de Castle R. *The content analysis of dreams*. New York: Appleton-Century-Crofts; 1966.
  53. Hall C, Nordby V. *The individual and his dreams*. New York: New American Library; 1972.
  54. Domhoff GW. *The scientific study of dreams*. Washington, DC: American Psychological Association; 2002.
  55. Pivik T, Foulkes D. *NREM mentation: relation to personality, orientation time, and time of night*. *J Consult Clin Psychol* 1968;32:144.
  56. Foulkes D. *Nonrapid eye movement mentation*. *Exp Neurol* 1967;(Suppl 4):28.

57. Wamsley EJ, Hirota Y, Tucker MA, et al. Circadian and ultradian influences on dreaming: a dual rhythm model. *Brain Res Bull* 2007;71:347.
58. Cavallero C, Cicogna P, Natale V, et al. Slow wave sleep dreaming. *Sleep* 1992;15:562.
59. Antrobus J. REM and NREM sleep reports: comparison of word frequencies by cognitive classes. *Psychophysiology* 1983;20:562.
60. Antrobus J, Kondo T, Reinsel R, et al. Dreaming in the late morning: summation of REM and diurnal cortical activation. *Conscious Cogn* 1995;4:275.
61. Verdone P. Temporal reference of manifest dream content. *Percept Mot Skills* 1965;20(Suppl):1253.
62. Baekeland F, Resch R, Katz D. Presleep mentation and dream reports. I. Cognitive style, contiguity to sleep, and time of night. *Arch Gen Psychiatry* 1968;19:300.
63. Natale V, Battaglia D. Temporal dating of autobiographical memories associated to REM and NREM dreams. *Imagination, Cognition, and Personality* 1990-91;10:279.
64. Grenier J, Cappeliez P, St-Onge M, et al. Temporal references in dreams and autobiographical memory. *Mem Cognit* 2005;33:280.
65. Nielsen TA, Powell RA. The 'dream-lag' effect: a 6-day temporal delay in dream content incorporation. *Psychiatr J Univ Ott* 1989;14:561.
66. Wamsley EJ, Tucker M, Payne JD, et al. Dreaming of a learning task is associated with enhanced sleep-dependent memory consolidation. *Curr Biol* 2010;20:850.
67. Siegel JM. The REM sleep-memory consolidation hypothesis. *Science* 2001;294:1058.
68. Vertes RP. Memory consolidation in sleep: dream or reality. *Neuron* 2004;44:135.
69. McClelland JL, McNaughton BL, O'Reilly RC. Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory. *Psychol Rev* 1995;102:419.
70. Spreng RN, Grady CL. Patterns of brain activity supporting autobiographical memory, prospection, and theory of mind, and their relationship to the default mode network. *J Cogn Neurosci* 2010;22:1112.
71. Schacter DL, Addis DR, Buckner RL. Remembering the past to imagine the future: the prospective brain. *Nat Rev Neurosci* 2007;8:657.
72. Winson J. The biology and function of rapid eye movement sleep. *Curr Opin Neurobiol* 1993;3:243.
73. Fiss H, Kremer E, Lichtman J. The mnemonic function of dreaming. *Sleep Res* 1977;6:122.
74. De Koninck J, Christ G, Hebert G, et al. Language learning efficiency, dreams and REM sleep. *Psychiatr J Univ Ott* 1990;15:91.
75. De Koninck J, Christ G, Rinfret N, et al. Dreams during language learning: when and how is the new language integrated. *Psychiatr J Univ Ott* 1988;13:72.
76. Cartwright R, Agargun MY, Kirkby J, et al. Relation of dreams to waking concerns. *Psychiatry Res* 2006;141:261.
77. Lara-Carrasco J, Nielsen TA, Solomonova E, et al. Overnight emotional adaptation to negative stimuli is altered by REM sleep deprivation and is correlated with intervening dream emotions. *J Sleep Res* 2009;18:178.
78. De Koninck JM, Koulack D. Dream content and adaptation to a stressful situation. *J Abnorm Psychol* 1975;84:250.