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Dreaming and Offline Memory Consolidation

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Abstract

Converging evidence suggests that dreaming is influenced by the consolidation of memory during sleep. Following encoding, recently formed memory traces are gradually stabilized and reorganized into a more permanent form of long-term storage. Sleep provides an optimal neurophysiological state to facilitate this process, allowing memory networks to be repeatedly reactivated in the absence of new sensory input. The process of memory reactivation and consolidation in the sleeping brain appears to influence conscious experience during sleep, contributing to dream content recalled on awakening. This article outlines several lines of evidence in support of this hypothesis, and responds to some common objections.

Keywords

Sleep; Dreaming; Rapid eye movement; Non-rapid eye movement; Memory consolidation; Offline processing; Memory reactivation; Replay; Consciousness

Introduction

Accumulating evidence suggests that memories are “consolidated” in the sleeping brain. Across a wide variety of memory domains—including verbal [1–4], emotional [5–7], motor [8, 9], perceptual [10], and spatial learning [11–14]—postlearning sleep has been shown to benefit later memory performance. Could dreams be a reflection of this memory processing during sleep? It has long been recognized that daily experience influences dreaming.

Even prior to psychoanalytic dream theory, early experimentalists postulated a systematic connection between waking experience and the content of our nightly dreams [15, 16]. As reviewed here, recent research confirms that dream content transparently reflects recently encoded memory. Meanwhile, recent discoveries in psychology and neuroscience suggest that the reactivation of memory networks during sleep aids consolidation, with both animal

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Compliance with Ethics Guidelines

Human and Animal Rights and Informed Consent This article does not report original research findings. Some studies described here were performed in our laboratory at Beth Israel Deaconess Medical Center, where all human subjects signed informed consent prior to participation.

and human studies demonstrating that patterns of brain activity first seen during learning are later "replayed" in sleep. Together, these data suggest that dreaming arises, at least in part, from the reactivation and consolidation of memory in the sleeping brain. In the following section, we will examine the evidence for this hypothesis, and explore several potential counterpoints.

Evidence Linking Sleep-Dependent Memory Consolidation with Dreaming

New Learning Experiences Are Incorporated into Dreams—A first clue to the relationship between learning, memory, and dreaming comes from the manner in which waking experience influences dream content. Although it may seem patently obvious that we dream about things experienced during the day, quantifying this phenomenon in the laboratory initially proved to be difficult. In the 1960s and 1970s, investigators endeavored to manipulate and predict the effects of specific waking experiences on dream content. But early attempts to influence dreams using manipulations such as films and images [17–20] were near uniform in their failure to detect statistically significant direct[1] effects of presleep stimuli on dream content (for a review, see [21]).

But these early studies were nonetheless informative. First, the laboratory setting itself was consistently found to have a powerful influence on dreams. Illustrating this robust effect, in an analysis of 813 rapid eye movement (REM) mentation reports collected across several studies, Dement et al. [22] reported that 22% of reports unambiguously incorporated either isolated elements (10%) of the laboratory situation (i.e., the experimenter, the sleep laboratory itself, electrodes, etc.) or more complete representations (12%) of the experimental setting (i.e., a combination of elements). In retrospect, this observation seems to indicate that the most salient aspects of our presleep experience are preferentially incorporated into dreaming. For research participants, the novel experience of sleeping in a strange laboratory with wires attached to their head may be a much more impactful event than any particular stimulus used as part of a psychological experiment.

Second, a handful of studies began to suggest that experimental manipulations involving exposure to novel learning experiences more easily affect subsequent dream reports. Roffwarg and coworkers [23, 24], for example, examined how the long-term use of red-tinted goggles impacted dreaming, finding evidence that this shift in waking color perception altered the reported perceptual qualities of dreaming. In analogous studies of long-term perceptual alteration, subsequent research examined dream reports during adaptation to the use of prism goggles that invert the visual field, similarly finding evidence for incorporation of perceptual alterations into subsequent dreaming [25, 26]. As discussed further later, studies by Fiss et al. [27] and De Koninck et al. [28] were likewise able to influence dreaming through the use of novel learning experience. The relative success of these paradigms, as opposed to the passive viewing of experimental stimuli before sleep, suggests that novel learning experiences have a particularly pronounced impact on dream experience.

[1]As opposed to "symbolic"

More recent studies have continued to demonstrate the effect of novel learning on dream content. Engaging, interactive video game tasks have shown particularly powerful effects. For example, in one study, participants played the video game Tetris extensively prior to dream report collection [29]. Mentation reports were then repeatedly elicited during early non-REM (NREM) sleep at sleep onset—64% of participants reported unambiguous[2] Tetris images. This basic effect of Tetris on sleep-onset imagery was later independently replicated by Kusse et al. [30]. Related investigations using a downhill skiing arcade game [31] and virtual navigation tasks [32, 33] have similarly demonstrated the robust incorporation of a presleep learning task into dream content. Although, for practical reasons, most of these studies have examined dream reports only from the first few minutes of NREM sleep, we have seen that this effect extends into later night dreaming during both stage 2 and REM sleep [34]. The frequency of direct incorporation in these sleep studies—which is dramatically higher than that observed in previous investigations—again suggests that *engaging learning experiences* may have a particularly robust influence on dream content, relative to viewing static images or films.

Other research has sidestepped the difficulty of prospectively manipulating dream content by asking participants to retrospectively identify the waking memory sources of dreams. For example, in an analysis of the possible waking memory sources of 299 home-collected dream reports, Fosse et al. [35] demonstrated that fragments of recent experience quite often appear in dream reports. In this study, 51% of 299 dream reports were judged by subjects to contain at least one feature with strong similarity to a recent waking event. Others have taken a similar retrospective approach, establishing that participants frequently identify recent memories as a source of dream content [36, 37], especially for dreams recalled from NREM sleep [38, 39]. These investigations highlight that although attempts to predict or control the waking source of specific dream elements have often failed, the influence of experience on dream content is nonetheless transparently clear.

Taken together, these data suggest that waking experiences are transparently represented in the content of dreams. Furthermore, it may be that particularly salient daytime experiences are preferentially incorporated into dreaming, with novel *learning* being a particularly strong driver of dream content.

Memories Are “Reactivated” in the Sleeping Brain

It is increasingly clear that sleep facilitates the consolidation of memory. A large number of studies have now replicated the robust finding that sleep following learning improves memory performance at a subsequent test [1, 3, 5, 8, 10, 40–43]. Recent discoveries in the neuroscience of learning and memory have been particularly enlightening in thinking about just *how* memory might be facilitated during sleep. Groundbreaking research in the last two decades has established the remarkable fact that waking patterns of brain activity are “replayed” during sleep in rodents [44–49]. For example, sequences of hippocampal place cell activity seen while rats explore a spatial environment during wakefulness are again observed when the rats fall asleep [48, 49]. As the firing of each of these hippocampal

[2]An example report from one participant: “[I'm] seeing in my mind how the game pieces kind of float down and fit into the other pieces, and am also rotating them.”

"place" cells is associated with a particular physical location in the environment, the reappearance of these sequences suggests that during sleep rats are retracing the paths they have learned. Initially described in the hippocampus, this effect was later seen in cortical regions as well [44, 46]. Although reactivation on the single neuron level has not yet been observed in humans, imaging studies demonstrate that brain regions engaged during presleep learning are again preferentially activated during sleep, and that this learning-related activity predicts postsleep task improvement [50, 51].

The discovery of memory reactivation during sleep certainly suggests a parallel with dreams of recent experience. Perhaps rats are dreaming of the "maze" they traversed while awake. Of course, we know that not all brain activity is consciously experienced. The neural activity associated with regulation of respiration and heart rate, for example, does not influence our stream of conscious awareness. Analogously, these cellular firing sequences in small regions of rodent hippocampus and cortex may be irrelevant to understanding the stream of consciousness during sleep. But is this so-called memory "replay" during sleep at least a good potential candidate for a neural correlate of dreaming? A complete review of the memory reactivation literature is beyond the scope of this article, but it is noteworthy that several key features of this phenomena parallel the structure of dream experience:

1. In rodent studies, memory reactivation has most often been reported to occur in NREM sleep. As described earlier, NREM sleep is also the sleep stage during which episodic memories are most often incorporated into dreaming.

2. Within NREM sleep, reactivation is expressed most strongly immediately after learning. The strength of this reactivation effect then tends to decay quickly across time [49, 52]. Similarly, sleep mentation may be most strongly related to recent experience early in the sleep phase [29, 31, 53].

3. Learning-related neural activity is not reactivated exactly in its original form. Waking firing sequences are reactivated in intermittent bursts, on a faster timescale than the original experience [49]. And rarely is a waking firing sequence reiterated exactly—although reactivated sequences statistically resemble waking activity, the "replay" is not always precise. Similarly, recent experiences are not "replayed" in dream content in their original form. Instead, dreams intermingle fragments of recent experience with other content [31, 35].

Dreaming About Learning Experiences Is Associated with Enhanced Memory

Memory reactivation during sleep is thought to lead to consolidation and enhancement of postsleep memory performance [54]. If dreaming reflects memory reactivation, we might expect that dreams should "index" the consolidation process, tracking the extent to which a particular memory is processed during sleep. In fact, evidence dating back to the 1970s suggests that dreaming of a learning experience is associated with enhanced memory for that information. Fiss et al. [27], for example, found that after reading the text of a short story, participants who reported dreams related to the story exhibited superior memory for the text the following morning. De Koninck et al. [28] also examined dreams and verbal learning, exploring dream content as a corollary of language learning in an academic setting. Among students enrolled in a French-immersion class, those with the strongest language acquisition across the 6-week course incorporated French into dream content more often than students who were less successful in the class. Most recently, our laboratory has demonstrated that dreaming of a virtual maze navigation task is associated with enhanced consolidation of spatial memory both across a nap [32] and across a full night of sleep [34]. Demonstrating that dreaming of a recent learning experience is associated with enhanced memory, these studies suggest that dream content does reflect the consolidation process.

Together, these observations lead us to the hypothesis that reactivation of memory traces during sleep causes memory-related content to be incorporated into dreams. As an index of memory reactivation, learning-related dreaming predicts subsequent memory performance. In this sense, dreaming may be considered a reflection of the consolidation process. In the following section, addressing several counterpoints will help us in further specifying the hypothesis and its predictions.

Objections to the Hypothesis

Dreams Are Not an Accurate Replay of Waking Experience

It is sometimes argued that dreams could not reflect an adaptive process of memory consolidation because they fail to faithfully replicate waking experience [55, 56]. Vertes [55], for example, has argued that “the hypothesis that sleep serves a role in memory consolidation would be more appealing if dreams reproduced waking experiences (or even approximately so), but they do not.” The late dream researcher Ernest Hartmann [56] similarly argued that the content of dreams is incompatible with memory consolidation because dream reports do not veridically replay waking experience.

It is true that episodic memories are rarely or never “replayed” in dreaming exactly as they occurred. Instead, dreams often incorporate only isolated fragments of a waking episode, and these may be interleaved with remote and semantic memory material. For example, although Fosse et al. [35] reported that more than half of dreams contained features similar to a recent experience, less than 2% of these preserved the original setting, characters, objects, and actions of the waking memory source. Consider the following example of a waking memory source and corresponding report (taken from [35]):

> *Waking experience*: “When I left 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...”
>
> *Corresponding dream experience*: “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...”*

Here, it would certainly be maladaptive for the dreamer to falsely remember having been in a room filled with muffins while shopping with her father—a fantastical event that never occurred.

But increasingly, we are learning that the effect of sleep on memory is not merely to cement experience in its original form. Instead, sleep transforms memory traces over time, allowing us to extract generalizations [57, 58], integrate information [41, 59], and arrive at creative insights [40, 60]. Models of memory consolidation have long stressed the integration of new information into established networks—the influential "complementary learning systems" model, for example, proposes sleep as a time when recently encoded information is "interleaved" into related memory networks [61]. This could be achieved by simultaneously reactivating recent and remote memory fragments, slowly associating new content into cortical semantic networks. Lewis and Durrant's recent information overlap to extract model of memory consolidation similarly postulates that sleep facilitates schema development through the repeated reactivation of related information [62••]. As in the example above, dream reports often bizarrely intermingle recent experience fragments with related material —this may be exactly the type of process that facilitates information integration during sleep.

The rodent memory reactivation literature also supports this conclusion. Studies of memory "replay" in rodents do *not* demonstrate reactivation of experience in its original form. First, learning-related patterns of activity are reactivated with some degree of distortion. But also, there is evidence that multiple related experiences are reactivated *simultaneously* during sleep [49]. This recombination of waking experiences could create an amalgam that serves to facilitate insight and generalization—in fact, it has recently been observed that replay can include the playing out of novel spatial trajectories never experienced while awake, some of which are "shortcuts" through a learned environment [63].

Thus, although dreams do not faithfully replay waking experience, we should not expect them to. Memory consolidation is not thought to involve the repeated replay of experience in its original form. To the contrary, sleep facilitates integration across multiple memories and the extraction of generalities. The intermingling of memory fragments seen in dream reports could well reflect this adaptive process.

Memory Reactivation Is a Poor Candidate for the Neural Correlate of Dreaming Because It Does Not Happen in "Real Time"

During rodent sleep, the reactivation of waking sequences occurs on a much faster timescale than the original experience [44, 49]. In contrast, there is compelling indirect evidence that dream events occur on the same timescale as waking experience [64]. This mismatch suggests that the brain processes of memory consolidation cannot be strictly *identical* to those that create dreaming. Still, it may be that memory reactivation *influences* dream content. The brief, localized bursts of memory reactivation observed in rodent models could feed into the dream creation process by affecting downstream mechanisms of dream generation. In short, memory reactivation as observed in rodents is not likely to be "the" neural mechanism of dreaming, but it may nonetheless be an important contributor.

Not All Dreaming Is Even Tangentially Related to a Past Memory

Only a portion of dream content can be definitively traced back to a specific prior experience [35, 38]. Dreams about possible futures, fantastical places, and people that we have never met may show no evidence of being tied to any *episodic* memory. But in a broader sense, all dreams (and all waking thought, for that matter) are most certainly constructed from *prior experience*. The appearance of a complete stranger in a dream, for example, relies on knowledge of the visual characteristics of the human face and on schemas for typical human behavior. This *semantic* memory has been generalized and extracted over the course of our lifetimes on the basis of thousands of individual past experiences. In a sense, this form of generalized memory can be thought of as the end product of consolidation. Through consolidation, individual experiences are integrated in order to extract commonalities [38, 61]. Certainly, the activation of semantic memory networks during sleep could occur independently of any consolidation-related process, perhaps reflecting more or less random activation of distributed cortical networks [65]. But alternatively, activation of semantic knowledge during sleep could reflect the "updating" of cortical networks as new information is slowly incorporated into existing schemas (e.g., as described in the information overlap to extract model [62••]).

However, the fundamental claim of the memory consolidation hypothesis—that dreaming reflects consolidation in the sleeping brain—does not require that all dream content result from memory-related activity. It may be that the activity of memory systems comprises only a portion of the total brain activity underlying dreaming, with diffuse activity unrelated to memory also influencing conscious experience during sleep. The most fundamental form of the hypothesis would not claim that every part of every dream can be explained as a memory-related process—only that memory consolidation is one major influence on dreaming.

Dreams Do Not *Seem* Functional

The content of dreams often does not seem particularly helpful. The philosopher Owen Flanagan [66] wrote that "since we rarely dream about what we need to remember, the hypothesis that dreams themselves serve any memory enhancing function appears unwarranted." Certainly, as in the example above, dreams typically do not appear to be a rehearsal of things that are important to remember. Although anecdotal evidence of dreams containing insight, creativity, and problem-solving abounds, empirical data are lacking. In fact, most dream reports contain negative emotions, failures, or misfortunes [67]. No problems are solved, no insights are arrived at, no fears are overcome. The bizarre and apparently irrelevant content of dreams has inspired proposals that we dream in order to forget spurious associations [68], or that the content of dreams is determined in an essentially random fashion [65]. In short, the content of recalled dreams does not in itself reveal any obvious function.

But a dream that arises from a functional brain process need not *seem* functional in itself. Supposing that memory consolidation does influence dreaming, this would not necessarily lead dreams to seem positive or helpful in any way. Memory consolidation involves the stabilization of recently formed memories against interference, as well as the functional reorganization of memory representations in the brain—these processes should not be expected to give rise to conscious experiences that mimic the waking experience of memorization, problem-solving, or creative insight. It is important to distinguish the functionality of memory processing during sleep from the notion that the content of dreams itself is functional—the former may be true without the latter.

It is not clear whether dreaming per se has a function at all. The data reviewed here suggest only that dreaming is influenced by brain processes that have a clearly demonstrated function—as memories are processed in the sleeping brain, this functional activity influences the ongoing content of a dream. To understand whether dreaming itself can be described as having a function, we will need first to understand the degree to which the brain basis of memory consolidation overlaps with the neural substrate for dreaming. Beyond this, a "function" for dreaming additionally hinges on the difficult question of whether conscious experience in general serves any function. Here, we suggest only that conscious experience during sleep is *influenced* by a neurophysiological function of the sleeping brain.

Conclusions

More than 50 years after the discovery of REM sleep launched the field of sleep research, the study of dreaming remains in its infancy. In recent years, however, new insights into the neurobiology of memory have led to the hypothesis that dreaming reflects the reactivation and consolidation of memory in the sleeping brain. In its most plausible form, this hypothesis asserts that:

1. Waking experiences do not appear in dreams in their original form, and we should not expect them to. Memory consolidation involves the integration of multiple experiences and the extraction of generalities. In dreams, the intermingling of memory fragments into novel and sometimes bizarre combinations could reflect this adaptive process.

2. The brain mechanisms of dreaming are likely not identical to those responsible for memory consolidation. Although the content of dreams is influenced by memory consolidation, it may be that not every element of every dream is related to this process. If conscious experience during sleep is the emergent result of neural activity distributed across much of the brain, only a portion of this activity would be expected to be influenced by the activity of memory systems.

3. Dreaming reflects the functional brain process of memory consolidation, but this does not mean that dreams, per se, have a function.

As for waking conscious experience, a single cognitive or brain system is unlikely to provide a complete explanation for the complexity of subjective experience during sleep. Ultimately, it may be that only a portion of dream experience originates from the consolidation of memory. And even for this portion, we have not yet arrived at a satisfying explanation. The evidence described here tells us that memory consolidation likely influences dream experience, but says little about exactly how this might occur. To *explain* the role of memory in dreaming, we need to arrive at a more complete understanding of how memory consolidation is instantiated in the brain and how it interacts with the neural substrate for dreaming. Even given these qualifications, however, the memory consolidation hypothesis provides a framework for moving forward with the study of subjective experience during sleep. Far from being a meaningless distraction, dreams may reflect an adaptive process by which new learning is stabilized and integrated with our existing knowledge. As such, the content of these experiences could provide an important and unique source of information about the functions of the sleeping mind and brain.

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