



PERSPECTIVES

Memory, Sleep, Dreams, and Consciousness: A Perspective Based on the Memory Theory of Consciousness

Andrew E Budson (1), Ken A Paller (1)³

¹Center for Translational Cognitive Neuroscience, Veterans Affairs Boston Healthcare System, Boston, MA, USA; ²Boston University Alzheimer's Disease Research Center, Boston University, Boston, MA, USA; ³Department of Psychology and Cognitive Neuroscience Program, Northwestern University, Evanston, IL, USA

Correspondence: Andrew E Budson, Neurology Service, VA Boston Healthcare System, 150 S. Huntington Ave, Boston, MA, 02130, USA, Email abudson@bu.edu

Abstract: Insights into the mysteries of dreaming and waking conscious experience can be gained by considering fundamental concepts in memory research. To support this assertion, we first provide an overview of the conscious/nonconscious distinction in memory research and then summarize the memory theory of consciousness (MToC). According to the MToC, the brain system responsible for explicit memory is also responsible for all our conscious experiences—perceptions, thoughts, memories, imaginings, and dreams. Ordinarily, we experience a continuity of consciousness, even when we wake from a period of sleep. On the other hand, memory dysfunction can disrupt this continuity across sleep and lead to disorientation upon awakening. The relationship between sleep and consciousness comes into sharper focus when considering the proposition that most sleep-based memory processing is below the surface of what we can experience. During sleep, stored information is reactivated in the service of memory consolidation and, unlike dreams, this memory processing remains in the realm of implicit memory. We further propose that many multifarious memories can be simultaneously reactivated through this sleep-based processing, engaging both the hippocampus and cerebral cortex. At the same time, fragments of information from a subset of reactivated memories may be strung together to create a consciously experienced storyline or dream. In keeping with the MToC, we emphasize that conscious experiences, both while awake and while dreaming, are not read-outs of external reality even though they are typically experienced as such. Sensory experiences seem direct and instantaneous, but they are indirect and delayed because they require sensory processing to reach the explicit-memory system. Furthermore, because we remain oblivious to the unconscious memory processing that pervades our sleep, people generally underestimate the impact of sleep on our subsequent recollections and habits in the wake state. In sum, memory research enriches our understanding of consciousness in many ways.

Keywords: explicit memory, consolidation, memory theory of consciousness, Alzheimer's disease, lucid dreams, targeted memory reactivation

Memory and Sleep

Over the past 50 years, a consensus developed among memory researchers about different forms of memory. A major distinction is between *explicit forms of memory*, which entail conscious remembering, and *implicit forms*, which do not.¹

Implicit or unconscious forms of memory include a variety of subtypes.¹ A basic list of subtypes includes (1) procedural memory or skill learning (eg, riding a bicycle); (2) cognitive skill learning (eg, learning to read words shown in a mirror-reversed font); (3) priming (facilitated processing due to a prior experience with the same or a related stimulus, eg, when memory of an advertisement unconsciously influences a decision); (4) classical conditioning (when a stimulus produces a bodily response due to a learned association, eg, Pavlov's dog salivating to a bell); (5) operant conditioning (when a behavior is emitted based on prior reward contingencies, eg, pressing a lever because doing so previously was rewarded); (6) habituation and sensitization (forms of nonassociative learning whereby responses change following repetition).¹

Explicit or conscious forms of memory have also been divided into subtypes. The epitome is *episodic memory*, when one recalls to mind an event from some prior time in one's life, from the recent past to long ago. Episodic memories can be retrieved with a strong feeling of remembering the prior episode, a *conscious recollection*, which has been likened to

1957



mental time-travel.² Sometimes elements of an episode are remembered less completely and/or less vividly, and in the extreme one might regard a stimulus pertaining to a prior episode as familiar without knowing why.³

Information can also be consciously remembered and disconnected from any specific episode (ie, *semantic memory*, as in knowing the temperature that water boils). We can also hold information in mind and manipulate it (ie, *working memory*, as in performing mental calculations). Working memory is the entry point for life episodes that are stored as episodic memories, and it is the usual exit point for retrieval of both episodic and semantic memories. Most researchers consider working memory conscious by definition although there are alternative views on this point. Another term used by memory researchers is *declarative memory*, which maps onto explicit memory and is conventionally defined as the ability to consciously recall or recognize facts and events.

When episodic memories are strongly connected to a person's life outside an artificial laboratory environment, the term *autobiographical memory* is often used. Like other episodic memories, autobiographical memories are a blend of episodic and semantic memories, in addition to numerous other cognitive functions. When the dreams of participants in a dream-diary study were classified as either episodic (including an aspect of autonoetic consciousness—time traveling back to the original event) or autobiographical (including aspects of experiences related to waking life), the investigators found that more than 80% of dreams incorporated autobiographical memory features, while less than 1% of dreams incorporated an episodic memory with autonoetic consciousness. The crux of this finding, consistent with the earlier findings of Fosse et al, is that dreams tend to be based on fragments of memories rather than on the re-experience of any single, unitary episode.

Sensory memory is memory for sensory impressions lasting approximately 0.5 to 2 seconds. The majority of our senses are "always on", even though much of this sensory processing goes on unconsciously. If you are speaking with a friend when entering a crowded and noisy room full of other conversations, most of those other conversations are processed unconsciously and then quickly forgotten within about 2 seconds. However, if your name is spoken within your earshot, the sensory memory sensation enters your working memory as an auditory perception and not only can you hear your name easily but you can generally recall the earlier part of the sentence in which your name was spoken. Thus, sensory memory could also be considered a form of conscious memory in that sensory impressions can be held in mind briefly or even brought back to mind as in the example above. On the other hand, the impact of sensory memory may be experienced consciously through the operation of working memory. By this view, sensory memory would be considered a source of information for explicit memory but not formally a part of the brain system that mediates explicit memory. That is, sensory memory could theoretically operate on its own without conscious experiences of perception.

Learning also entails multiple stages. When information is first encountered, it must be encoded in the sense of forming a memory trace that can later be retrieved (recalled, recognized, or otherwise used). Specialized processes also occur in-between encoding and retrieval. These processes determine whether a memory is stored securely, stored in a precarious form, or forgotten. This critical in-between process is known as consolidation, 9,10 and it occurs with episodic memories as well as with other forms of memory such as procedural memories. Consolidation can also change aspects of an episodic memory. A memory might be strengthened such that it is easier to retrieve later and it might be integrated with other memories to produce a blended or even distorted memory. As this integration occurs, the emotional intensity of a troubling episode might thereby be reduced, although sometimes this integration can lead to heightened emotional intensity when it becomes linked with maladaptive schemas, leading to post-traumatic stress disorder (PTSD). 11,12 Often a key result of consolidation is to reduce the extent to which recall remains dependent on the hippocampus, which can occur in conjunction with transforming a detailed episode to its gist, lacking some of the contextual features. 13 When the hippocampus is dysfunctional and the cerebral cortex mostly intact, people typically remain able to recall well-learned events that they experienced long ago. Note that when memories are retrieved, they are generally re-encoded and they may then undergo what some investigators have termed a "reconsolidation" process that can further change the stored memory. 14-16 On the other hand, many views of consolidation encompass the changes that so-called reconsolidation could produce, such that a separate function is not required. ^{17,18} In this sense, consolidation includes both memory strengthening and memory transformation, and it can continue indefinitely, with optional pauses, along either a straight or a tortuous path, such that additional change is always a possibility.

Consolidation can transpire during intentional rehearsal, waking rest, and sleep. Here, we focus on sleep-based consolidation. A central aspect of our position is that sleep-based consolidation occurs unconsciously and in parallel



across many cortical regions simultaneously. Consistent with this view, evidence from a study by Schectman et al showed that, during NREM sleep, multiple memories can be reactivated without the bottleneck or limited capacity that characterizes conscious experience.²⁰ Many distinct memories can apparently be reactivated simultaneous without interfering with each other. We thus infer that reactivation was unconscious in this experiment. By extension, and in keeping with the fact that people seem oblivious to overnight memory processing, a reasonable speculation (expanded upon further below) is that memory reactivation during sleep is generally unconscious.

Advances have also been made in understanding the physiology of sleep-based consolidation. For example, post-sleep remembering correlates with the total time in intervening non-rapid eye movement sleep (NREM) sleep and with slow-wave power, whereas disrupting slow-wave physiology reduces later recall. Other studies linked spindles during NREM stages 2 and 3 sleep to memory replay and consolidation. The evidence about REM sleep and memory processing has been less consistent, but REM may be important to help us link recent episodic memories to older ones and to our semantic memory store of facts and knowledge, as discussed further below. Sleep-based increases in connections and associations between memories are perhaps indirectly responsible for subsequent improvements in creativity and problem solving. The process of the physiology of sleep-based consolidation. For example, post-sleep remember sleep (NREM) sleep and with slow-wave power, 21,22 the evidence about REM sleep and memory processing has been less consistent, but REM may be important to help us link recent episodic memories to older ones and to our semantic memory store of facts and knowledge, as discussed further below. Sleep-based increases in connections and associations between memories are perhaps indirectly responsible for subsequent improvements in creativity and problem solving.

Dreams occur during both NREM and REM sleep,²⁷ but a consensus view has not emerged about why we dream.^{28–36} Jonathan Winson's classic book on this topic, *Brain and Psyche*,³⁷ made the case that REM-sleep dreaming is critical for memory consolidation and a landmark paper by Robert Stickgold et al³⁸ subsequently made the case that new neuroscientific methodologies can link offline memory reprocessing with sleep and dreaming. Based on our perspective from memory research, we consider dreaming as a by-product of sleep-based consolidation. As postulated above, memory processing during sleep happens largely unconsciously, when many memories are reactivated simultaneously to benefit consolidation—but at the same time a conscious experience can be synthesized based on a creative assembly of a small subset of those memories. By this notion, dream contents include some memory fragments that are reactivated in the service of consolidation, but additionally, a narrative structure is produced to provide a storyline for the experience. This storyline itself may or may not be part of consolidation. Dreams can touch on small portions of recent learning, such as fragments of yesterday's waking experiences, but over the course of 7 or 8 hours of nocturnal sleep, memory fragments come from progressively earlier time periods.²⁷ Our view is that the many memory associations relevant for consolidation are unconsciously reactivated, whereas the dream storyline is consciously experienced when a tenuous subset of fragments of those reactivated memories is pieced together.

Dreams can be bizarre and non-sensical, although thought-like cognition without a narrative storyline is also common during sleep. One proposal about why bizarre dreams occur during REM sleep is that this brain state is particularly conducive to developing distant associations between memories.³⁹ The evidence supporting this proposal was obtained after people woke up, not during sleep. Following REM awakenings, priming was stronger for distant (eg, *crime-gun*) compared to proximal associations (eg, *hot-cold*); following NREM awakenings, priming was stronger for proximal compared to distant associations, as also observed during wake.

From a memory perspective, sleep can be understood as critically important for normal memory function, given the lasting ramifications of consolidation. The work of consolidation is in the establishment of new connections, anchoring recent memories within relevant knowledge networks. When this happens during sleep, there may also be some conscious experience synthesized as this memory processing unfolds—that is, dreaming. While this plasticity of new connections is clearly important for memory function, we must entertain the possibility that perhaps dream experiences are not. The ability to remember what transpired during a dream is optional, and for most people dream recall is more the exception than the rule. By this view, dreams reflect a storyline generated to make sense of a subset of the activated memory fragments. Most importantly, in the present context, the work of seeking new connections in the service of consolidation can go forward in parallel across the whole cerebral cortex, without the constraints that come with conscious experience. The advantage of unconscious processing is that many thoughts and ideas can be activated at the same time, through massive parallel processing. The dream, on the other hand, is limited to a sequence of discrete cognitive combinations amenable to working memory. From this standpoint, dreams reflect some small portion of overnight memory work.

Thus, two views on the issue of the relationship between dreams and consolidation can be juxtaposed. By the view we put forward above, unconsciously activated information is central to consolidation while dreams per se add little more.

The obvious alternative is that dreams are also critical for consolidation. Can the available empirical evidence adjudicate between these two views? Let us say some specific dreamt material is linked to consolidation based on data from subsequent memory performance; how would we know whether the consolidation connection comes from that conscious dream directly—or instead due to unconscious material that prompted the dream? At this point, the situation seems to be a stalemate, as this sort of evidence cannot unequivocally implicate dreams or rule them out as contributors to consolidation. Yet, researchers continue to investigate the possible relevance of dreaming for waking cognition, such as by using sensory stimulation during sleep (eg, 40,41). Whereas dreams can also be influenced by pre-sleep manipulations, any post-sleep repercussions of those manipulations could be attributed to prior brain activity either during sleep or wake. Stimulation during sleep avoids such experimental confounds. Notably, the process of remembering a dream can naturally influence memory storage in the same way that remembering any episode can influence memory storage.

The Memory Theory of Consciousness (MToC)

With this background in place, we will now summarize the memory theory of consciousness (MToC). A more thorough presentation was given by Budson, Richman, and Kensinger. 42 For present purposes, a core idea is that the brain system that generates all of our conscious experiences is the very same system used to give us explicit memory (the confluence of episodic, semantic, and working memory, as described above). People typically think of memory as a function superimposed on perception and based on the results of perception. The MToC turns that around, postulating instead that the very awareness we have of sensory analysis, of perception, is based on the operation of this memory system. In other words, the sensory information that constitutes an event is assembled at encoding and consequently can be remembered later. This assembling is akin to what Anthony Marcel described in his constructivist framework. 43 Assembling conscious contents takes high-level sensory processing from all modalities and synthesizes the ongoing progression of events we experience, and we experience them precisely because they have been assembled in this way. Without this process, we would only have unconscious perceptions and implicit memories. An anonymous reviewer pointed out to us that the synthetic process described in the MToC is similar to an idea from the first edition of Kant's 1781 Critique of Pure Reason, 44 in which Kant identifies in the "Deduction of the Categories"—the synthesis of apprehension in intuition, the synthesis of reproduction in imagination, and the synthesis of recognition in a concept. 45,46 Kant's syntheses can be interpreted as a precursor to the idea put forth in the MToC that temporally extended, multimodal representations must be integrated within a unified subjectivity for experience to be coherent (AEB was a philosophy major in college and did study the entire Critique of Pure Reason, so it is certainly possible that this part of the MToC unconsciously stemmed from Kant). Other views that are consistent with these ideas include those of Hinze Hogendoorn, who suggests that there is no natural boundary between perception and memory, 47 and Donna Rose Addis, who argues that perception, memory, and imagination all involve the creation of a simulation, and only the simulation is consciously experienced.⁴⁸

Memory can, however, be dissociated from perception. Patients with amnesia due to damage to the hippocampus, adjacent cortex, or other regions such as the medial diencephalon can display a relatively circumscribed amnesia. They seem to perceive normally and be cognitively intact except that they are impaired in (a) forming new explicit memories, and usually also in (b) retrieving a subset of previously acquired explicit memories. For this widely accepted conceptualization of amnesia to fit with the MToC, we must note that the explicit memory system is not entirely destroyed in these cases. Working memory functions as does retrieval for well-established episodic and semantic memories. Perceptual consciousness can rely on these remaining aspects of the memory system. Most experiences of the present moment may play out normally but are tainted by difficulties in remembering. The strong dissociation observed in cases of circumscribed amnesia is between their impaired memory abilities and otherwise preserved conscious experience. This dissociation is consistent with an important tenet of the MToC, which is that each aspect of consciousness will have its own neuroanatomy and neural correlate. Thus, patients with amnesia have lost one aspect but not all aspects of their conscious experience.

The explicit memory system, according to the MToC, has the unique function of binding the elements of an experience together, thus creating the stream of consciousness and allowing for memories of experiences to be stored and later retrieved. The fact that we have a stream of experiences at all is thus attributed to this memory system. Relevant additional tenets of the MToC are as follows: (1) Conscious perceptions, decisions, and actions are memories of



unconscious sensations, decisions, and actions, delayed by 350 to 500 ms, a time frame for conscious perceptions, decisions, and actions supported by many empirical studies. 47,50-53 (2) Conscious deliberation can influence the unconscious decisions and actions that are made. (3) The neuroanatomical source of consciousness maps onto the neuroanatomical localization of explicit memory, which potentially includes the entire cerebral cortex.⁵⁴ (4) Thalamic nuclei likely operate as hubs, selectively activating cortical regions to enable different aspects of cognitive processing to be actualized as conscious experiences. (5) Disorders of the cerebral cortex will disrupt consciousness including epilepsy, migraine, cortical strokes, and Alzheimer's disease and other cortical dementias.⁵⁵

The MToC differs from the prevailing theories of consciousness, although it is consistent with many key aspects of them. Re-entry, local recurrence, and predictive processing theories emphasize how top-down signaling predicts the causes of bottom-up sensory signals, with continuous feedback and feedforward processes occurring to minimize prediction errors.⁵⁶ For example, local recurrence theory suggests that localized recurrent or re-entrant processing in perceptual cortices can enable consciousness, whereas parietal and frontal regions are used to report the perceptual experience and/or use the perceptual experience for reasoning and decision making.^{57,58} In predictive processing theories, conscious perception is the brain's "best guess" of the source of the sensory information it is receiving. 56 The MToC is consistent with the suggestion that processing in perceptual cortices is sufficient for consciousness, but the MToC suggests that other regions of cortex (including frontal cortex) are also sufficient for consciousness.⁴² The idea espoused by predictive processing theories that conscious perception is the culmination of feedback and feedforward processes is consistent with the MToC. MToC would simply emphasize that the top-down predictions are based on episodic and semantic memory.⁴²

Global neuronal workspace theory suggests that sensory information has access to consciousness when it is broadcast in a neuronal workspace across higher-order cortical association areas in a fronto-parietal network. Information in working memory that is attended to become conscious by using the global workspace for broadcast. 56,59 The MToC is in agreement with most of the basic tenets of global neuronal workspace theory. As we noted earlier, it is in working memory that bottom-up sensory memories and top-down episodic and semantic memories can lead to conscious experiences, consistent with longstanding views on memory. 60-62 Pivotal differences between the theories are (a) that the MToC considers subcortical regions (such as the thalamus) as critical hubs, rather than fronto-parietal regions, and (b) that the MToC suggests that consciousness developed as part of explicit memory, such that the purpose of consciousness aligns with the purpose of explicit memory—to use acquired information to understand the present moment, imagine various possible futures, and plan accordingly.

Perceptual reality monitoring theory seeks to explain how we know the difference between the perception of external reality versus internal imagination or dreaming.⁶³ An explanation is needed because the neural regions and networks involved in perceiving and imaging are quite similar.⁶³ Dysfunction of this system may occur, which can lead to believing that a dream actually happened or to hallucinations. One paper suggests that in order to know the difference between perceiving, imagining, and dreaming, higher-level circuits (such as the anterior medial prefrontal cortex) evaluate first-order sensory signals in primary sensory cortices while taking into account the contributions of top-down control mechanisms to determine the source of a sensory experience. 63 We would note that this theory developed, in part, from the memory research and reality-monitoring framework of Marcia Johnson et al. This framework was created to explain how we distinguish remembered events that were actually experienced from those that were merely imagined. 64,65 It should thus not be surprising that the MToC is generally consistent with the perceptual reality monitoring theory. However, perceptual reality monitoring theory invokes what memory researchers refer to as post-retrieval verification and monitoring, which a person can use to determine the veracity of a recalled memory. In this sense, perceptual reality monitoring theory focuses on how we metacognitively know that an experience is real, whereas we would argue that the MToC goes further and naturally addresses our seemingly instantaneous subjective experiences of reality.

Higher-order theories argue that a mental state is conscious because it is the target of a certain kind of metarepresentational state. A representation might be "seeing a green light", while a corresponding meta-representation might be "I have an experience of seeing a green light". Most higher-order theorists suggest that consciousness is dependent on prefrontal cortex.⁶⁶ From the MToC perspective, higher-order theories are reasonable descriptions and explanations for self-consciousness, but the MToC argues that "first-order" processes can be conscious without meta-representations.

Lastly, we consider Daniel Dennett's Multiple Drafts theory of consciousness.⁶⁷ Although it is not currently considered one of the prevailing theories of consciousness, it is relevant for this paper. In brief, Dennett suggests that there is no truth of what is conscious or unconscious until a subject provides a report of an experience; only then can we answer the question of what that subject was conscious of. Before that time, Dennett explains that the brain is doing a lot of unconscious parallel processing when the drafts are being updated as raw sensory information continues to enter the brain. This theory is partly consistent with the MToC if we view the "multiple drafts" as akin to unconscious bottom-up and top-down processing that generates the contents of memory producing consciousness. We differ from Dennett in that we do not believe it is necessary to wait until there is a report of an experience to determine what is in consciousness. Most relevant to the present paper, however, is the fact that the multiple drafts theory notes that the majority of perceptual processing occurs unconsciously, and a perception is only "finalized" when it is reported. This notion bears some similarity to the idea that the majority of sleep-based memory consolidation occurs unconsciously while, during this consolidation process, an occasional set of memory fragments develops a narrative structure and can be consciously experienced and sometimes later reported as a dream upon awakening.

To summarize this section, although the MToC differs from prevailing theories of consciousness, it is consistent with many key aspects of them. The MToC agrees with re-entry and local recurrence theories, in that processing in perceptual cortices can be sufficient for consciousness but would also argue that the same applies for other regions of cortex, including prefrontal cortex. Predictive processing and multiple drafts theories and the MToC all agree that conscious perception is the culmination of feedback and feedforward processes, although the MToC emphasizes that the top-down predictions are based on episodic and semantic memory. The MToC and global neuronal workspace theory agrees that information in working memory is conscious, although the MToC emphasizes that it is bottom-up sensory memories and top-down episodic and semantic memories that lead to conscious perceptual experiences. An additional difference is that global neuronal workspace theory suggests that fronto-parietal regions are the critical hubs, whereas MToC suggests that the thalami are the hub. The perspective of the MToC, perceptual reality monitoring theory and higher-order theories provide a good explanation of self-consciousness and other aspects of metacognition, but they do not provide an explanation of moment-to-moment subjective experience of reality that usually seems real without any metacognitive effort. Thus, although agreeing with key aspects of each of these other theories of consciousness, the MToC disagrees with some of their details and provides an overarching framework for conceptualizing consciousness, which is that consciousness is fundamentally a feature of the brain's episodic memory system.

The Continuity of Consciousness Across a Period of Sleep

A fundamental property of conscious experience is that it seems continuous from one moment to the next. This experience of continuity is remarkable, given that our days are often fragmented as our attention is rapidly diverted from one thing to the next, whether by external events or internal thoughts. It is even more remarkable that we generally experience this continuity when we wake from sleep in the morning. Insofar as we think of ourselves as conscious beings à la Descartes, ⁶⁸ we think of ourselves as the same being when we wake in the morning as when we went to sleep the night before. Many consciousness theorists have emphasized sleep. Patricia Churchland noted that the "most basic experience we all have of the difference between being conscious and not being conscious is falling asleep". ⁶⁹ How do we manage to recover from the interlude of slumber? It is, of course, memory that allows us to experience this feeling of continuity.

To unpack this memory-consciousness connection further, consider again the principal postulate of the MToC that consciousness is a function of the explicit memory system. The explicit memory system is not only required for explicit memory—it is also required for our ability to consciously perceive the world around us, understand what is happening, and make conscious decisions that lead to actions. Thanks to the explicit memory system, sensory impressions can reach consciousness, and we can think about what is happening in the world. In the process of consciously perceiving the world, we rely on working memory to maintain and manipulate the information, on semantic memory to make sense of it, and on episodic memory to relate the current situation to prior episodes and understand the current context.

Thus, when I wake in the morning, it is memory that allows me to experience myself as the same person who went to bed the night before. I can remember my past experiences and what they mean in the sense of a sequence defining my existence spreading out over time. Episodic memory enables me to remember why I set the alarm 30 minutes earlier than usual (a plane to catch) and why I am wearing these ridiculous pajamas (packed the usual pair for the trip). Semantic



memory maintains my sense of self, including that I am a professor, a spouse, and a parent. The next morning, when I wake in a hotel room, episodic memory enables me to recall my arrival to the hotel, the city I am in now, and the face of my new grandchild that I saw yesterday for the first time.

Memory Dysfunction and Discontinuity

If episodic memory is needed for this continuity of the conscious self to be present upon awakening, individuals with impaired explicit memory should show impairment in this continuity. This unfortunately happens frequently when individuals with middle-stage Alzheimer's disease travel and wake up in a hotel room in the morning. While they are at home in an environment where they have lived for a long time, implicit memory and well-established episodic memories enable them to function appropriately. Repeated priming of their environment yields a sense of familiarity. Thanks to consolidation, some cortically based memories enable accurate remembering of episodes from long ago. A patient might remember decorating their home 30 years ago, for example. Procedural memory helps them to brush their teeth, bathe, dress, and make breakfast. So long as they are in their usual residence where they see their usual cues that prompt them to perform their usual routines, they function normally and experience continuity in their conscious awareness.⁷⁰

When individuals with middle-stage Alzheimer's disease travel to a new environment, like a retirement community or when on vacation, their experience of consciousness can also remain continuous. They experience one event after another: they pack their bags at home, travel to the airport, board the plane, walk off the plane, travel to their accommodations, get ready for bed, and go to sleep. They can make sense of each moment with their intact working memory, with weak explicit memories, and by making inferences based on what they perceive in the moment. When they wake in the morning, however, because of dysfunctional episodic memory, their ability to recall yesterday's events is faulty such that they tend to experience disorientation. They cannot explain why they find themselves in an unfamiliar environment. Some routines of procedural memory (such as personal hygiene habits) may be easily transferrable from their home to the new environment. 11 However, intact procedural memory may not suffice when the usual sensory cues are not present and episodic memory is not functioning well.

Most importantly for our discussion, an individual with this sort of memory impairment can feel very disoriented in a new environment.⁷² They may be troubled because things do not feel familiar. After a delay, especially an overnight delay, they may have forgotten traveling to the new location. Priming and other forms of implicit memory may be present, but alone they may be insufficient for producing familiarity. Thus, when they wake in the morning and look around, the room does not feel familiar. They automatically search their episodic memory for clues as to where they are now. However, their episodic memory is dysfunctional, and they often cannot recall their travels from the day before. Consequently, they cannot link experiences of their normal routines at home, which could be quite solid, with their present conscious experience. The end result is a troubling sense of disorientation. Such individuals may frantically call family members (perhaps repeatedly), asking where they are and to come get them, or they may leave their room searching for something familiar, risking becoming lost in the new environment. A moderate or severe impairment in explicit memory can make it very difficult to reestablish the continuity of conscious experience in such circumstances.

Experiencing the Present, Awake or Asleep

Multiple types of memory help us to experience the continuity of consciousness. Waking from a period of sleep is a prime opportunity for disorientation due to the lack of continuity. Another circumstance that could potentially produce disorientation is when we pause to imagine engaging in some other activity removed from the present environment. For example, we might vividly imagine a possible event in the future or recollect an event from the past. In the latter case, we can re-live an event as it happened or imagine it happening a little differently. Simulated or imagined experiences like these take us out of the present moment, requiring a critical contribution from the prefrontal cortex.⁷³ Furthermore, memory is critical for jumping around from one simulation to another or back to the context of the present moment, and to do so without disorientation. Reality monitoring is important in these situations, as we differentiate real from imagined experiences to keep track of what really did or did not happen. If we do not constantly stay tied to the present moment, we can easily become disoriented—if not for our memory abilities to help make sense of these discontinuities of experience. The most common experience of these discontinuities is when we become distracted as we walk from one room to the next—and then cannot remember what we were going to do in the room we have just entered.

We also have simulated experiences when we dream, but they tend to be much more immersive than anything imagined while awake. The potential for being disoriented should be greatly magnified following a dream. Also, dreams can be so realistic that it is surprising we do not more often think our remembered dreams actually happened. Maybe that is because remembered dreams typically have a distinctive ending—"and then I woke up". They are thus tagged as not having actually happened. Normally, the continuity of consciousness after waking from a dream is generated by the same memory-based mechanisms described above.

Where do dreams come from? This question has long perplexed humanity. People throughout history have given many sorts of answers, including omens from God or messages from the ancestors. Some individuals, from students to saints, have charted a new course for their future based on their dreams. Western civilization and Abrahamic religions have felt this influence, as evidenced by the dreams of Jacob, Pharaoh, and others from the bible, for example. More recently, Freudian traditions put a lot of stock into the notion that dreams hold keys for understanding our own minds. Thomas Edison, Salvador Dali, surrealist authors, and others used dreaming and liminal states to unlock their own creativity.

The position we have taken here is that sleep enables massive reactivation of memories in parallel, unconsciously, to aid consolidation. REM sleep may be particularly amenable to seeking new connections across memories, as distant associations are prioritized and many memory fragments are simultaneously activated in the service of revealing potentially useful new connections. At the same time, separate from all this unconscious memory reactivation, a storyline can be formed—our brains excel at that, they do it all day long. The storyline is the only portion of sleep-based consolidation subject to the constraint of the limited capacity of working memory, and the only conscious portion. Although people can gain insight through a deep examination of their dreams, ⁷⁴ we do not favor the view that dream interpretation is a royal road to anywhere. Rather, the tactic that is prominent in current memory research is to investigate the role of sleep in memory processing and in related cognitive functions, considering the neural substrates and potential repercussions of that processing, and including dreaming to the extent that it could potentially shed additional light on these larger questions.

Can dreams provide a "peek-under-the-hood" to potentially gain insights into the big questions of consciousness? This is a notion that many researchers and philosophers have entertained.^{75–77} When we dream, we feel that we are experiencing a sequence of events taking place in the "outside world" rather than "in our heads" (as in imagined experiences). Our dreams do not come with a fuzzy border and harp music, as they might in a children's TV show or cartoon, but rather they are mostly as believable as any waking experience. Prior to awakening, we generally mistake our dreams for waking reality.

When we are awake and perceiving the world, our conscious experiences give us a direct read-out of what is going on at that moment—seemingly. The notion that we experience a conscious read-out of what is happening in the world around us seems completely intuitive and valid. And yet, from the first-person perspective, the very same type of experience—sensing a world—takes place in a dream. How can wake experiences be direct reflections of the sensory world at that moment while comparable dream experiences are created by the brain based on novel combinations of fragments of memories from the past? The answer must be that our experiences are always constructed by the brain; the very same processing that gives us dreams gives us waking experiences of reality. In other words, our brains do not need incoming sensory input to produce realistic experiences. Our waking experiences are the way that they are not because of sensory input but because of the functional capabilities of the human brain. The MToC argues that the functional capability that produces our experience of reality, whether we are awake or asleep, is the explicit memory system.

During sleep, we speculate that our brains are simply carrying on with functioning akin to what happens when we are awake. The typical modes of action of the human brain persist across wake and sleep. While we are awake, our brains are producing a stream of experiences of being in the world, punctuated by thoughts. While we are asleep, without the tremendous barrage of sensory input to constrain experience, perhaps our brains tend to return to these waking habits, producing a stream of experiences in the world punctuated by thoughts.

If dreaming reflects only a small portion of the memory fragments reactivated for consolidation, the way these fragments are put together with a storyline may not be a part of the work of consolidation. This view could be conceived



of as an extension of the MToC explanation for waking perception. According to the MToC, we do not have direct conscious experiences of perceiving reality, making decisions, or performing actions. Instead, we do all these activities unconsciously, and then we consciously access them after the fact (perhaps 350 to 500 ms later); our conscious experiences all arise from the explicit memory system. 42 We fail to notice this delay, as it is our normal way to operate. Perceptions, decisions, and actions reach our conscious mind after the fact and are referred backwards in time.

The Experience of Knowing We Are Asleep

Whereas the prior discussion has pointed to ways in which the experience of dreaming and the experience of being awake have much in common, there are important differences. Waking consciousness is constrained by sensory input in a way that sleeping consciousness is not. Remarkably, we tend to misconstrue dreams, even when they go in bizarre directions, as experiences of waking reality. Upon awakening, we may then realize it was a dream, retrospectively. The exception when we recognize the dream as a dream while still dreaming—is known as a lucid dream.

Approximately half the people in a large survey reported having experienced a lucid dream at least once, and 20% reported having a lucid dream at least once a month. 78 Lucid dreaming is a first step to gaining some control over the dream. People often find lucid dreams very enjoyable. Some seek them out for recreation, solving problems, practicing skills, or as a treatment for nightmares. ^{79–81} A person can wake up and report that they experienced a lucid dream a short time earlier, but lucid dreaming can also be verified physiologically in real time. For example, polysomnographic records can show a period of REM sleep while the individual emits a pre-arranged pattern of eye movements to indicate that they know they are dreaming.⁸²

Recent investigations of lucid dreaming have documented that dreamers can respond to questions posed by experimenters by producing responses to those questions, a phenomenon known as interactive dreaming.⁸³ Lucid dreams can also be provoked at home when sensory cues are paired with pre-sleep cognitive training. 84 With the development of wireless sleep-monitoring technology, we are now able to gather evidence of volitional signals during sleep in the home environment rather than only in the sleep lab. With these advances, what could future studies of lucid dreaming tell us about conscious experience?

The answer to this question could guide future thinking about the MToC. One valuable line of research could attempt to determine how waking consciousness differs from sleep consciousness. We may often be conscious while awake and unconscious while asleep, but there are important exceptions. We are conscious while dreaming and we may be conscious during many stages of sleep. 85 Neuroscientists face a big challenge when people wake up with no recollection of sleep-based experience because there are two logical possibilities. One possibility is that they were asleep without dreaming or having any experiences; another is that they were conscious while asleep but woke up having forgotten those experiences. Therefore, it is difficult to verify dreamless sleep, that is, to be certain that a period of sleep in any sleep stage transpired with no conscious awareness. Research could instead focus on characterizing sleep experiences more thoroughly so as to highlight how they differ from waking experiences.

Interestingly, there can be ambiguity about whether a person was awake or asleep during a particular period of time. Sleep research currently relies on firm criteria for rating any period of 30 seconds as awake or asleep according to the orthodox polysomnographic methods that have been in place for many decades. Often there are very distinctive signals of awakening confirmed by very distinctive experiences of awakening. But other times the situation is muddy. In paradoxical insomnia, patients experience being awake for periods of time that are polysomnographically rated as sleep. Which is correct, the sleep physiology or the person's report? Perhaps people can experience a stream of thoughts, maybe recurring worries, sometimes worries about not being asleep, and these thoughts may occur during sleep. A broader definition of dreaming includes the usual sorts of autobiographical and often-bizarre narratives as well as periods of a progression of thoughts without an immersive environmental context.⁸⁶ When this sort of thinking occurs during sleep, it could be perceived as wake (which formerly was termed sleep-stage misperception instead of paradoxical insomnia). Whatever the terminology, these periods of sleep may not be optimally restful or restorative. For present purposes, the conclusion is that a variety of experiences can transpire during sleep.

Sleep amnesia is a term that explicitly draws attention to our poor ability to remember the events of sleep (although this term is not widely used, we would advocate its usefulness). Sleep amnesia is entirely different from the amnesia following specific neurological insult or disease, but it may be akin to *infantile amnesia*, which recognizes our generally poor ability to remember the events of early childhood. We wake up oblivious to the contents of most of our dreams and sometimes even to the fact that we had dreams overnight. There are exceptions to this; some people develop exceptional dream-recall abilities. Still, everyone sleeps while not privy to the cyclic patterns of light sleep to deep sleep to REM sleep that we repeat each night. We are also oblivious to *microarousals*, actually waking up briefly during sleep. We may have amnesia for these very common events, momentarily stopping and then re-starting sleep, because the sleeping brain shifts to a special mode not conducive to forming new memories. The brain may even be in this mode in the moments before sleep onset, though memory deficits may require that a few minutes of sleep follows. Forgetting seems to be the rule—and remembering the exception—for what happens during sleep and during immediately preceding time periods. From the perspective of the MToC, when we shift from awake to asleep, the explicit memory system may shift from being amenable to storing new memories to consolidating existing memories.

The MToC also connects to the contemporary notion of *local sleep*—that different parts of the brain may concurrently be in different states. This notion defies the commonsense view that a person is either awake or asleep, that sleeping is a state of a whole person. The MToC argues that different cortical regions enable different aspects of consciousness and that each cortical region has the potential for an autonomous experience. Interestingly, REM sleep may start earlier in the hippocampus than the cortex—by more than 17 seconds on average—which may have implications for memory formation and remembering dreams. The possibility that lucid dreaming results when parts of the brain (eg, prefrontal cortex) reach an awake state, however, has been controversial. On a wider scale, birds and cetaceans can sleep with one hemisphere at a time. however, has been controversial sleep are less clear-cut and currently difficult to confirm as the local neural signals defining wake and sleep are not fully characterized.

A standard way of portraying lucidity is that some processing associated with the frontal lobes is enhanced—particularly the ability to assess whether events are logical, follow a sensible progression, or concur with normative waking experiences. In contrast, this type of processing is generally weak during nonlucid dreams. Although we cannot say if the frontal lobes are "more awake" during lucid dreams, there is an improvement in some operations thought to be frontally supported. The notion of cortical sleep and wake activity having regional cortical localization is supported by scalp and intracranial EEG recordings that find sleep-like and wake-like activity simultaneously in different cortical regions. ^{94–96}

Perhaps, the state of being asleep or awake should apply only to a whole organism, not to a single neuron or network of neurons. Likewise, we do not know if it makes sense to consider a single brain region as a conscious piece of tissue because we cannot specify the minimal ingredients for a conscious experience. Yet, there are certainly states when novel combinations are present (eg, sleep-walking, sleep-talking, and other parasomnias). If there can simultaneously be some cortical regions functioning in a sleep mode and others functioning in a wake mode, there is also merit to the possibility that some regions of cortex contribute to conscious experience at a given moment, while others do not. If we accept that individual cortical regions can potentially be autonomously conscious (ie, contributing to a person's experience at that moment), we must then explain how the limited capacity of conscious working memory is imposed across the cerebral cortex.

Studies of coma patients provide another source of support for the notion espoused in the MToC that many cortical regions can support conscious experience independently. It has been discovered that up to 20% of behaviorally unresponsive patients in the intensive care unit are "covertly" conscious, that is, they are conscious but have no ability to communicate that they are. Such individuals with covert consciousness (typically from a traumatic brain injury) have been able to respond to questions by imagining engaging in different activities, such as playing tennis or navigating in their home to respond to "yes" or "no" to questions, respectively. Thus, covert consciousness provides another example, like lucid dreaming, where the typical dichotomy of being "conscious, awake, and responsive" versus "unconscious, not awake, and unresponsive" breaks down.

Strategically Influencing the Sleeping Mind

In dreams, as conceptualized here, top-down interpretive processes linked with conscious experience intrude into the free-wheeling mixed-up gathering of memories brought up unconsciously for consolidation. Turning this upside down, a novel line of research over the past 15 years has focused on how bottom-up sensory processes can intrude into sleep to strategically alter memory storage. In some cases, sensory influences during sleep remain unconscious, whereas other times not.



One of the first examples of dream modification through the experimental presentation of sensory information was described by Jean Marie Léon d'Hervey de Saint-Denys in his 1867 book, Les Rêves et les Moyens de les Diriger. 98 Hervey de Saint-Denys would purchase perfumes when he traveled to different places and, at each place, he would smell the purchased scent throughout his trip. After taking several trips over a period of weeks or months, he would ask his servant to put a few drips of one of the perfumes on his pillow while he was sleeping, without knowledge of which night his servant would do it. Hervey de Saint-Denys described examples of how he dreamed of experiences and scenes associated with the trip in which he had smelled that particular perfume.⁹⁹

Over the past decades, many studies have sought to strategically influence sleep cognition. 100,101 One example comes from Rudoy et al, who taught participants to associate 50 unique object images with 50 specific locations on a computer screen. 102 Each image was paired with its naturally related sound, such as whistle with kettle. Participants heard 25 of the paired sounds while napping during NREM sleep; EEG recordings confirmed both NREM sleep and that the sounds were played softly enough to avoid waking the participants. Upon awakening, participants were asked to move each object image to its specific location using a computer mouse. Most of the participants (10 of 12) showed more accurate placement for the images whose sound was presented while sleeping compared with the images whose sounds were not presented. 102 Interestingly, participants were at chance when asked to guess which sounds were presented while they were sleeping. Yet, this result does not unequivocally show that people did not consciously perceive sound cues presented during sleep, given the aforementioned concept of sleep amnesia. In other words, people may forget experiences they have during sleep NREM sleep when cues are presented. Alternatively, slow waves may not be conducive to conscious experience during sleep, as argued on the basis of sleep-EEG observations prior to a post-awakening dream report by Francesca Siclari et al^{103,104} along with studies from Marcello Massimini et al of the Perturbational Complexity Index derived from EEG responses to pulses of transcranial magnetic stimulation during wake, sleep, and other altered states. 105-107

More than 2000 subjects have now participated in these Targeted Memory Reactivation (TMR) studies in over 90 experiments, confirming that presenting sounds, spoken words, or odors during stage 2 NREM and slow-wave sleep (ie, stage 3 NREM) can enhance memory retrieval for the associated items upon awakening. Most of these studies did not include dream reports, although one exception is the study by Antony et al. 108 who found that musical cues during NREM sleep led to an improvement in accuracy when participants played the corresponding melody in a task resembling the Guitar Hero video game, and one participant spontaneously reported dreaming of a visually similar experience. TMR studies in REM sleep have yielded mixed findings that have not yet produced a coherent picture. There have been some intriguing results 109,110 that future research could follow up, including investigations using TMR to selectively influence dreaming. 40,41

Although Hervey de Saint-Denys experienced a remembered dream that involved associated memories from his waking life, TMR experiments provide robust evidence that no conscious recollection is required for sensations processed during sleep to influence our ability to recall associated information. TMR evidence suggests that memory reactivation, whether consciously experienced and remembered or not, is the "motive force" in strengthening memories and determining which memories will be available for later retrieval. 111 Furthermore, memory reactivation is likely operative whether provoked by stimulation or occurring naturally.

From the MToC perspective, TMR studies show that memory storage can be altered unconsciously during sleep through bottom-up sensory processes. These changes in our brains consequently influence our subsequent conscious experiences while awake. For example, some memories may more easily come to mind due to enhanced memory consolidation. Our conscious waking experiences are thus influenced by unconscious processing during sleep, paralleling the ways in which our conscious waking experiences can be influenced by implicit memory.

Conclusion

Although experiences do not have a location, theories of consciousness have long struggled with specifying relevant anatomical sources in the brain. A strength of the MToC is its emphasis on the brain's explicit memory system because memory researchers have learned much about the underlying anatomy. Information from potentially anywhere in the cerebral cortex is eligible, with the involvement of connected diencephalic structures and with the hippocampus playing a key role in linking cortical memory components together. In this article, we showed how an emphasis on the explicit memory system also sheds light on sleep, dreaming, and consciousness.

During sleep, the brain shifts to a special mode that is (a) conducive to memory consolidation and (b) not conducive to forming new memories. We acquire an abundance of new memories every day when we are awake. Only a fraction of these memories will be useful later, but it is challenging to know which. As often hypothesized, memory consolidation handles this problem through gradual changes in information storage in the brain. 9,17,18,37 When this process is working well, the challenges that we face and the problems that we need to solve nudge consolidation to potentially relevant information. Overnight, memories from the prior day are fresh, so they tend to be reactivated. Effective memory storage favors those new memories that are well integrated with existing memories. Sleep-based consolidation engages massive memory reactivation so that fruitful associations can be established. Such associations can thus lead to effective storage. Our proposal here, in the context of the MToC, is that all this overnight memory processing occurs unconsciously, due to this special mode of the explicit memory system.

In short, the sleeping brain is poor at laying down new memories because it is instead taking on the work of reorganizing existing memories, unconsciously. Dreams seem to be an exception. Dreams are undoubtedly influenced by which memories are reactivated during sleep, but dreams are not the primary substance of sleep-based consolidation. Dreams are a single track of conscious experience whereas, according to the views put forward here, sleep-based consolidation occurs unconsciously and widely in parallel across all cortical regions.

The study of dreams can be informative in this context because dreams mirror the conscious experience of being awake and aware in the world—but in these cases the world is constructed from memory influences instead of perceptual influences. Particularly promising approaches to the study of dreams can include in-depth first-person interviews 112 as well as other novel methods. 86 Although there is a long history of using sensory stimulation to influence dreams, 100 future studies are likely to expand this work to touch on many questions about dreaming, including how it is based on memory storage and how it may change memory storage.

Dreams subjectively feel like experiences of waking reality. Most people rarely experience a dream while knowing that they are dreaming. The exceptions, lucid dreams, can be used in further investigation of these ideas. For example, a postulate of the MToC is that cortical regions have the potential to support independent conscious experiences, and at any given moment some regions contribute to conscious experiences while others do not. Interactive dreaming makes it possible to gain neurophysiological information while simultaneously recording signals from the dreamer to convey what they are experiencing at that moment.

Exciting prospects are on the horizon for additional ways to study conscious experiences, taking into account both wake and sleep. Humans have been hampered in research on consciousness because we rely so much on our own experiences to guide our understanding. Memory research has shown that implicit memory must be included when we describe how memory works. More broadly, implicit cognitive processing is foundational for understanding cognition. By the same token, sleep research has a fundamental role for the study on consciousness even though it is off the radar when we first consider what it is like to have a conscious experience.

Dreaming by our view stands apart from sleep-based unconscious memory consolidation, but it is nonetheless a valuable focus for consciousness research. Sometimes, remembered dreams develop importance beyond their role in memory processing. We believe it is our personal interpretation of memories of our dreams that enables dreams to influence our waking conscious experience. In this way, most dreams, remembered or not, could be entirely epiphenomenal, while some remembered dreams can be meaningful or even enlightening. Zadra and Stickgold have suggested an alternative view.⁹⁹ They hypothesize that even non-remembered dreams play an important role in waking life beyond memory consolidation, one in which novel, creative, and previously unmade associations can be consciously experienced while asleep. They suggest that the conscious experience, even if completely forgotten, is important for several reasons, including determining how the "dreamer's mind" responds to different aspects of the dream. Their concept of the importance of the conscious experience of all dreams, even those forgotten, may be correct and is worthy of further study.

Whether or not the tenets of the MToC are supported by future investigations, there is certainly value to bringing together disparate fields of study as exemplified here. We can find clues about consciousness in many places. Moreover, as exemplified by the present analysis, a fruitful way to produce valuable scientific progress is to bring together the separate phenomena of memory, sleep, dreams, and consciousness.



Abbreviations

MToC, memory theory of consciousness; NREM, non-rapid eye movement sleep; PTSD, post-traumatic stress disorder; REM, rapid eye movement sleep; TMR, Targeted Memory Reactivation.

Data Sharing Statement

No new data was generated for this paper.

Author Contributions

CRediT: AEB: Conceptualization, funding acquisition, methodology, project administration, writing – original draft. KAP: Conceptualization, funding acquisition, investigation, writing – reviewing and editing. All authors gave final approval of the version to be published; have agreed on the journal to which the article has been submitted; and agree to be accountable for all aspects of the work.

Funding

This work was supported by a US Veterans Affairs Clinical Science, Research & Development Merit Review Award (CX002400 to AEB), the National Institute on Aging (P30 AG072978 to AEB), the National Science Foundation (BCS-2048681 to KAP), and the National Heart, Blood, and Lung Institute (DP1 HL179370 to KAP).

Disclosure

Andrew Budson reports grants from the National Institute on Aging and Veterans Affairs Department of Research. The other author report no conflicts of interest in this work.

References

- 1. Budson AE, Kensinger EA. Why We Forget and How to Remember Better: The Science Behind Memory. Oxford University Press; 2023.
- 2. Tulving E. Episodic and semantic memory. In: Organization of Memory. Vol 1. Academic Press; 1972:381-403.
- 3. Eichenbaum H, Yonelinas AP, Ranganath C. The medial temporal lobe and recognition memory. Annu Rev Neurosci. 2007;30(1):123-152. doi:10.1146/annurev.neuro.30.051606.094328
- 4. Trübutschek D, Marti S, Ojeda A, et al. A theory of working memory without consciousness or sustained activity. eLife. 2017:6:e23871. doi:10.7554/eLife.23871
- 5. Squire LR. Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. Psychol Rev. 1992;99(2):195-231. doi:10.1037/0033-295X.99.2.195
- 6. Fan C, Simpson S, Sokolowski H. Autobiographical memory. 2022. doi:10.31234/osf.io/9c6b8
- Malinowski JE, Horton CL. Memory sources of dreams: the incorporation of autobiographical rather than episodic experiences. J Sleep Res. 2014;23(4):441-447. doi:10.1111/jsr.12134
- 8. Fosse MJ, Fosse R, Hobson JA, Stickgold RJ. Dreaming and episodic memory: a functional dissociation? J Cogn Neurosci. 2003;15(1):1-9. doi:10.1162/089892903321107774
- 9. Paller KA. Consolidating dispersed neocortical memories: the missing link in amnesia. Memory. 1997;5(1-2):73-88. doi:10.1080/741941150
- 10. Paller KA. Memory consolidation: systems. In: Squire LR editor. Encyclopedia of Neuroscience. Academic Press; 2009:741–749. doi:10.1016/ B978-008045046-9.00770-1
- 11. Cohen RT, Kahana MJ. A memory-based theory of emotional disorders. Psychol Rev. 2022;129(4):742-776. doi:10.1037/rev0000334
- 12. Bogie BJ, Persaud MR, Smith D, Kapczinski FP, Frey BN. Explicit emotional memory biases in mood disorders: a systematic review. Psychiatry Res. 2019;278:162–172. doi:10.1016/j.psychres.2019.06.003
- 13. Paller KA, Antony JW, Mayes AR, Norman KA. Replay-based consolidation governs enduring memory storage. In: Poeppel D, Mangun GR, Gazzaniga MS, editors. The Cognitive Neurosciences. 6th ed. The MIT Press; 2020:263-274. doi:10.7551/mitpress/11442.003.0031
- 14. Alberini CM, LeDoux JE. Memory reconsolidation. Curr Biol. 2013;23(17):R746-R750. doi:10.1016/j.cub.2013.06.046
- 15. Nader K, Hardt O. A single standard for memory: the case for reconsolidation. Nat Rev Neurosci. 2009;10(3):224-234. doi:10.1038/nrn2590
- 16. Yassa MA, Reagh ZM. Competitive trace theory: a role for the hippocampus in contextual interference during retrieval. Front Behav Neurosci. 2013;7. doi:10.3389/fnbeh.2013.00107
- 17. Dudai Y. The restless engram: consolidations never end. Annu Rev Neurosci. 2012;35(1):227-247. doi:10.1146/annurev-neuro-062111-150500
- 18. Paller KA. Recurring memory reactivation: the offline component of learning. Neuropsychologia. 2024;196:108840. doi:10.1016/j. neuropsychologia.2024.108840
- 19. Paller KA, Creery JD, Schechtman E. Memory and sleep: how sleep cognition can change the waking mind for the better. Annu Rev Psychol. 2021;72(1):123-150. doi:10.1146/annurev-psych-010419-050815
- 20. Schechtman E, Antony JW, Lampe A, Wilson BJ, Norman KA, Paller KA. Multiple memories can be simultaneously reactivated during sleep as effectively as a single memory. Commun Biol. 2021;4(1):25. doi:10.1038/s42003-020-01512-0



- Marshall L, Helgadóttir H, Mölle M, Born J. Boosting slow oscillations during sleep potentiates memory. Nature. 2006;444(7119):610–613. doi:10.1038/nature05278
- 22. Ngo HVV, Martinetz T, Born J, Mölle M. Auditory closed-loop stimulation of the sleep slow oscillation enhances memory. *Neuron*. 2013;78 (3):545–553. doi:10.1016/j.neuron.2013.03.006
- 23. Roüast NM, Kumral D, Gais S, Schönauer M. Random auditory stimulation disturbs traveling slow waves and declarative memory. *bioRxiv*. 2025;2025–02.doi:10.1101/2025.02.06.636865
- 24. Antony JW, Piloto L, Wang M, Pacheco P, Norman KA, Paller KA. Sleep spindle refractoriness segregates periods of memory reactivation. Curr Biol. 2018;28(11):1736–1743.e4. doi:10.1016/j.cub.2018.04.020
- 25. Cairney SA, Guttesen AÁV, El Marj N, Staresina BP. Memory consolidation Is linked to spindle-mediated information processing during sleep. Curr Biol. 2018;28(6):948–954.e4. doi:10.1016/j.cub.2018.01.087
- 26. Sanders KEG, Osburn S, Paller KA, Beeman M. Targeted memory reactivation during sleep improves next-day problem solving. *Psychol Sci.* 2019;30(11):1616–1624. doi:10.1177/0956797619873344
- 27. Picard-Deland C, Konkoly K, Raider R, et al. The memory sources of dreams: serial awakenings across sleep stages and time of night. *Sleep*. 2023;46(4):zsac292. doi:10.1093/sleep/zsac292
- 28. Horton CL, Malinowski JE. Autobiographical memory and hyperassociativity in the dreaming brain: implications for memory consolidation in sleep. Front Psychol. 2015;6:6. doi:10.3389/fpsyg.2015.00874
- 29. Murkar A. Stage-dependent cortical/hippocampal reactivation may explain the differences in recall frequency between REM and NREM mentation. *International Journal of Dream Research*. 2013. doi:10.11588/IJODR.2013.2.10546
- 30. Murkar A, Smith C, Dale A, Miller N. A neuro-cognitive model of sleep mentation & memory. *International Journal of Dream Research*. 2014. doi:10.11588/IJODR.2014.1.10306
- 31. Paller KA, Voss JL. Memory reactivation and consolidation during sleep. Learn Mem. 2004;11(6):664-670. doi:10.1101/lm.75704
- 32. Payne JD, Nadel L. Sleep, dreams, and memory consolidation: the role of the stress hormone cortisol. *Learn Mem.* 2004;11(6):671–678. doi:10.1101/lm.77104
- 33. Wamsley EJ. Dreaming and offline memory consolidation. Curr Neurol Neurosci Rep. 2014;14(3):433. doi:10.1007/s11910-013-0433-5
- 34. Wamsley EJ, Stickgold R. Dreaming and offline memory processing. Curr Biol. 2010;20(23):R1010-R1013. doi:10.1016/j.cub.2010.10.045
- 35. Wamsley EJ, Stickgold R. Memory, sleep, and dreaming: experiencing consolidation. Sleep Med Clin. 2011;6(1):97–108. doi:10.1016/j. jsmc.2010.12.008
- Zhang Q. A computational account of dreaming: learning and memory consolidation. Cogn Syst Res. 2009;10(2):91–101. doi:10.1016/j. cogsys.2008.06.002
- 37. Winson J. Brain and Psyche: The Biology of the Unconscious. Anchor Pr./Doubleday, 1985.
- 38. Stickgold R, Hobson JA, Fosse R, Fosse M. Sleep, learning, and dreams: off-line memory reprocessing. *Science*. 2001;294(5544):1052–1057. doi:10.1126/science.1063530
- Stickgold R, Scott L, Rittenhouse C, Hobson JA. Sleep-induced changes in associative memory. J Cogn Neurosci. 1999;11(2):182–193. doi:10.1162/089892999563319
- 40. Konkoly KR, Morris D, Cho M, et al. Investigating dreams by strategically presenting sounds during REM sleep to reactivate waking experiences. *Neuropsychologia*. 2025:109229.
- 41. Konkoly KR, Morris D, Hurka K, Sanders K, Paller KA. Experimentally provoking dreams of unsolved puzzles during REM sleep boosts creative problem-solving. 2025. doi:10.31234/osf.io/du3bf v1
- 42. Budson AE, Richman KA, Kensinger EA. Consciousness as a memory system. Cogn Behav Neurol off J Soc Behav Cogn Neurol. 2022;35 (4):263–297. doi:10.1097/WNN.000000000000019
- Marcel AJ. Conscious and unconscious perception: an approach to the relations between phenomenal experience and perceptual processes. Cognit Psychol. 1983;15(2):238–300. doi:10.1016/0010-0285(83)90010-5
- 44. Kant I Critique of Pure Reason. Cambridge University Press; 1781. Available from: https://cpb-us-w2.wpmucdn.com/u.osu.edu/dist/5/25851/files/2017/09/kant-first-critique-cambridge-1m89prv.pdf. Accessed August 06, 2025.
- 45. Strawson PF. The Bounds of Sense: An Essay on Kant's Critique of Pure Reason. Methuen: 1966.
- 46. Allison HE. Kant's Transcendental Idealism: An Interpretation and Defense. Revised and enlarged ed. Yale University Press; 2004.
- Hogendoorn H. Perception in real-time: predicting the present, reconstructing the past. Trends Cogn Sci. 2022;26(2):128–141. doi:10.1016/j. tics.2021.11.003
- 48. Addis DR. Mental time travel? A neurocognitive model of event simulation. Rev Philos Psychol. 2020;11(2):233-259. doi:10.1007/s13164-020-00470-0
- 49. Cohen MA, Ortego K, Kyroudis A, Pitts M. Distinguishing the neural correlates of perceptual awareness and postperceptual processing. *J Neurosci.* 2020;40(25):4925–4935. doi:10.1523/JNEUROSCI.0120-20.2020
- 50. Herzog MH, Drissi-Daoudi L, Doerig A. All in good time: long-lasting postdictive effects reveal discrete perception. *Trends Cogn Sci.* 2020;24 (10):826–837. doi:10.1016/j.tics.2020.07.001
- 51. Libet B. Unconscious cerebral initiative and the role of conscious will in voluntary action. *Behav Brain Sci.* 1985;8(4):529–539. doi:10.1017/S0140525X00044903
- 52. Libet B, Alberts WW, Wright EW, Delattre LD, Levin G, Feinstein B. Production of threshold levels of conscious sensation by electrical stimulation of human somatosensory cortex. *J Neurophysiol*. 1964:27(4):546–578. doi:10.1152/in.1964.27.4.546
- 53. Libet B, Wright EWW, Feinstein B, Pearl DK. Subjective referral of the timing for a conscious sensory experience: a functional role for the somatosensory specific projection system in man. *Brain*. 1979;102(1):193–224. doi:10.1093/brain/102.1.193
- 54. Murray EA, Wise SP, Baldwin MKL, Graham KS. The Evolutionary Road to Human Memory. Oxford University Press; 2020:xiv,200.
- 55. Huntley JD, Fleming SM, Mograbi DC, et al. Understanding Alzheimer's disease as a disorder of consciousness. *Alzheimers Dement Transl Res Clin Interv.* 2021;7(1):e12203. doi:10.1002/trc2.12203
- 56. Seth AK, Bayne T. Theories of consciousness. Nat Rev Neurosci. 2022;23(7):439-452. doi:10.1038/s41583-022-00587-4
- 57. Lamme VAF. Towards a true neural stance on consciousness. Trends Cogn Sci. 2006;10(11):494-501. doi:10.1016/j.tics.2006.09.001
- 58. Lamme VAF. How neuroscience will change our view on consciousness. Cogn Neurosci. 2010;1(3):204-220. doi:10.1080/17588921003731586



- 59. Mashour GA, Roelfsema P, Changeux JP, Dehaene S. Conscious processing and the global neuronal workspace hypothesis. Neuron. 2020;105 (5):776–798. doi:10.1016/j.neuron.2020.01.026
- 60. Baddeley A. The episodic buffer: a new component of working memory? Trends Cogn Sci. 2000;4(11):417-423. doi:10.1016/s1364-6613(00) 01538-2
- 61. Baddeley A, Hitch GJ. Working memory. In: Bower GA, editor. The Psychology of Learning and Motivation. Vol 8. Academic Press; 1974:47-89.
- 62. Moscovitch M. Memory and working with memory: evaluation of a component process model and comparisons with other models. In: Schacter D, Tulving E, editors. Memory Systems. MIT Press; 1994:94.
- 63. Dijkstra N, Kok P, Fleming SM. Perceptual reality monitoring: neural mechanisms dissociating imagination from reality. Neurosci Biobehav Rev. 2022;135:104557. doi:10.1016/j.neubiorev.2022.104557
- 64. Johnson MK, Raye CL. Reality monitoring. Psychol Rev. 1981;88(1):67-85. doi:10.1037/0033-295X.88.1.67
- 65. Simons JS, Garrison JR, Johnson MK. Brain mechanisms of reality monitoring. Trends Cogn Sci. 2017;21(6):462–473. doi:10.1016/j. tics.2017.03.012
- 66. Lau H, Rosenthal D. Empirical support for higher-order theories of conscious awareness. Trends Cogn Sci. 2011;15(8):365-373. doi:10.1016/j. tics.2011.05.009
- 67. Dennett DC. Consciousness Explained. Little, Brown and Company; 1991.
- 68. Descartes R. Meditations on First Philosophy. 3rd ed. Hackett Publishing Company; 1641.
- 69. Churchland PS. Touching a Nerve: The Self as Brain. W. W. Norton & Company; 2013.
- 70. Budson AE, Solomon PR. Memory Loss, Alzheimer's Disease, and Dementia E-Book: A Practical Guide for Clinicians. 3rd ed. Elsevier; 2021.
- 71. Budson AE, Price BH. Memory dysfunction. N Engl J Med. 2005;352(7):692-699. doi:10.1056/NEJMra041071
- 72. Budson AE. Six Steps to Managing Alzheimer's Disease and Dementia: A Guide for Families. Oxford University Press USA OSO; 2021.
- 73. Knight RT, Grabowecky MF, Scabini D. Role of human prefrontal cortex in attention control. Adv Neurol. 1995;66:21–34;discussion34–36.
- 74. Blagrove M, Hale S, Lockheart J, Carr M, Jones A, Valli K. Testing the empathy theory of dreaming: the relationships between dream sharing and trait and state empathy. Front Psychol. 2019;10:1351. doi:10.3389/fpsyg.2019.01351
- 75. Metzinger T. Why are dreams interesting for philosophers? The example of minimal phenomenal selfhood, plus an agenda for future research. Frontiers in Psychology. 2013;4:746. doi:10.3389/fpsyg.2013.00746
- 76. Windt JM. How deep is the rift between conscious states in sleep and wakefulness? Spontaneous experience over the sleep-wake cycle. Philos Trans R Soc B Biol Sci. 2021;376(1817):20190696. doi:10.1098/rstb.2019.0696
- 77. Mallett R, Nahas Y, Christoff K, Paller KA, Mills C. Cognitive control and semantic thought variability across sleep and wakefulness. Philos Mind Sci. 2025;6. doi:10.33735/phimisci.2025.10307
- 78. Saunders DT, Roe CA, Smith G, Clegg H. Lucid dreaming incidence: a quality effects meta-analysis of 50 years of research. Conscious Cogn. 2016;43:197-215. doi:10.1016/j.concog.2016.06.002
- 79. De Macêdo TCF, Ferreira GH, De Almondes KM, Kirov R, Mota-Rolim SA. My dream, my rules: can lucid dreaming treat nightmares? Front Psychol. 2019;10:2618. doi:10.3389/fpsyg.2019.02618
- 80. Schädlich M, Erlacher D, Schädlich M, Schredl M. Applications of lucid dreams: an online study. Consciousness and Cognition. 2012;21 (3):1456–1475. doi:10.11588/IJODR.2012.2.9505
- 81. Stumbrys T, Erlacher D, Johnson M, Schredl M. The phenomenology of lucid dreaming: an online survey. Am J Psychol. 2014;127(2):191–204. doi:10.5406/amerjpsyc.127.2.0191
- 82. Baird B, LaBerge S, Tononi G. Two-way communication in lucid REM sleep dreaming. Trends Cogn Sci. 2021;25(6):427-428. doi:10.1016/j. tics.2021.04.004
- 83. Konkoly KR, Appel K, Chabani E, et al. Real-time dialogue between experimenters and dreamers during REM sleep. Curr Biol. 2021;31 (7):1417-1427.e6. doi:10.1016/j.cub.2021.01.026
- 84. Konkoly KR, Whitmore NW, Mallett R, Mazurek CY, Paller KA. Provoking lucid dreams at home with sensory cues paired with pre-sleep cognitive training. Conscious Cogn. 2024;125:103759. doi:10.1016/j.concog.2024.103759
- 85. Windt JM, Nielsen T, Thompson E. Does consciousness disappear in dreamless sleep? Trends Cogn Sci. 2016;20(12):871–882. doi:10.1016/j. tics.2016.09.006
- 86. Mallett R, Konkoly KR, Nielsen T, Carr M, Paller KA. New strategies for the cognitive science of dreaming. Trends Cogn Sci. 2024;28 (12):1105-1117. doi:10.1016/j.tics.2024.10.004
- 87. Nemeth G. The route to recall a dream: theoretical considerations and methodological implications. Psychol Res. 2023;87(4):964-987. doi:10.1007/s00426-022-01722-7
- 88. Wyatt JK, Bootzin RR, Anthony J, Bazant S. Sleep onset is associated with retrograde and anterograde amnesia. Sleep. 1994;17(6):502-511. doi:10.1093/sleep/17.6.502
- 89. Zeki S. The disunity of consciousness. In: Velmans M, Schneider S, editors. The Blackwell Companion to Consciousness. Vol. 168. 2007:379-388.
- 90. Durán E, Oyanedel CN, Niethard N, Inostroza M, Born J. Sleep stage dynamics in neocortex and hippocampus. Sleep. 2018;41(6). doi:10.1093/ sleep/zsv060
- 91. Baird B, Tononi G, LaBerge S. Lucid dreaming occurs in activated rapid eye movement sleep, not a mixture of sleep and wakefulness. Sleep. 2022;45(4):zsab294. doi:10.1093/sleep/zsab294
- 92. Lyamin OI, Mukhametov LM, Siegel JM, Nazarenko EA, Polyakova IG, Shpak OV. Unihemispheric slow wave sleep and the state of the eyes in a white whale. Behav Brain Res. 2002;129(1-2):125-129. doi:10.1016/S0166-4328(01)00346-1
- 93. Rattenborg NC, Amlaner CJ, Lima SL. Behavioral, neurophysiological and evolutionary perspectives on unihemispheric sleep. Neurosci Biobehav Rev. 2000;24(8):817–842. doi:10.1016/s0149-7634(00)00039-7
- 94. Nir Y, Staba RJ, Andrillon T, et al. Regional slow waves and spindles in human sleep. Neuron. 2011;70(1):153-169. doi:10.1016/j. neuron.2011.02.043
- 95. Nobili L, Ferrara M, Moroni F, et al. Dissociated wake-like and sleep-like electro-cortical activity during sleep. NeuroImage. 2011;58 (2):612-619. doi:10.1016/j.neuroimage.2011.06.032



- 96. Andrillon T, Burns A, Mackay T, Windt J, Tsuchiya N. Predicting lapses of attention with sleep-like slow waves. Nat Commun. 2021;12 (1):3657. doi:10.1038/s41467-021-23890-7
- 97. Fischer D, Edlow BL. Coma prognostication after acute brain injury: a review. JAMA Neurol. 2024;81(4):405. doi:10.1001/ jamaneurol.2023.5634
- 98. Hervey de Saint-Denys de JML. Les Rêves Et Les Moyens de Les Diriger [Dreams and How to Direct Them: Practical Observations]. 1867.
- 99. Zadra A, Stickgold R. When Brains Dream: Exploring the Science and Mystery of Sleep. First ed. W. W.Norton & Company; 2021.
- 100. Salvesen L, Capriglia E, Dresler M, Bernardi G. Influencing dreams through sensory stimulation: a systematic review. Sleep Med Rev. 2024;74:101908. doi:10.1016/j.smrv.2024.101908
- 101. Picard-Deland C, Bernardi G, Genzel L, Dresler M, Schoch SF. Memory reactivations during sleep: a neural basis of dream experiences? Trends Cogn Sci. 2023;27(6):568-582. doi:10.1016/j.tics.2023.02.006
- 102. Rudoy JD, Voss JL, Westerberg CE, Paller KA. Strengthening individual memories by reactivating them during sleep. Science. 2009;326 (5956):1079. doi:10.1126/science.1179013
- 103. Siclari F, Baird B, Perogamvros L, et al. The neural correlates of dreaming. Nat Neurosci. 2017;20(6):872-878. doi:10.1038/nn.4545
- 104. Siclari F, Bernardi G, Cataldi J, Tononi G. Dreaming in NREM sleep: a high-density EEG study of slow waves and spindles. J Neurosci. 2018;38(43):9175-9185. doi:10.1523/JNEUROSCI.0855-18.2018
- 105. Casali AG, Gosseries O, Rosanova M, et al. A theoretically based index of consciousness independent of sensory processing and behavior. Sci Transl Med. 2013;5(198):198ra105. doi:10.1126/scitranslmed.3006294
- 106. Casarotto S, Hassan G, Rosanova M, et al. Dissociations between spontaneous electroencephalographic features and the perturbational complexity index in the minimally conscious state. Eur J Neurosci. 2024;59(5):934-947. doi:10.1111/ejn.16299
- 107. Tononi G, Boly M, Cirelli C. CONSCIOUSNESS AND SLEEP. Neuron. 2024;112(10):1568-1594. doi:10.1016/j.neuron.2024.04.011
- 108. Antony JW, Gobel EW, O'Hare JK, Reber PJ, Paller KA. Cued memory reactivation during sleep influences skill learning. Nat Neurosci. 2012;15(8):1114-1116. doi:10.1038/nn.3152
- 109. Pereira SIR, Santamaria L, Andrews R, Schmidt E, Van Rossum MCW, Lewis P. Rule abstraction is facilitated by auditory cuing in REM sleep. J Neurosci. 2023;43(21):3838-3848. doi:10.1523/JNEUROSCI.1966-21.2022
- 110. Hutchison IC, Pezzoli S, Tsimpanouli ME, et al. Targeted memory reactivation in REM but not SWS selectively reduces arousal responses. Commun Biol. 2021;4(1):404. doi:10.1038/s42003-021-01854-3
- 111. Hu X, Cheng LY, Chiu MH, Paller KA. Promoting memory consolidation during sleep: a meta-analysis of targeted memory reactivation. Psychol Bull. 2020;146(3):218-244. doi:10.1037/bul0000223
- 112. Demšar E, Windt J. Studying dream experience through dream reports: points of contact between dream research and first-person methods in consciousness science. In: Dreaming and Memory: Philosophical Issues. Springer; 2024:85-117. doi:10.1007/978-3-031-68204-9_5

Nature and Science of Sleep

Publish your work in this journal

Dovepress Taylor & Francis Group

Nature and Science of Sleep is an international, peer-reviewed, open access journal covering all aspects of sleep science and sleep medicine, including the neurophysiology and functions of sleep, the genetics of sleep, sleep and society, biological rhythms, dreaming, sleep disorders and therapy, and strategies to optimize healthy sleep. The manuscript management system is completely online and includes a very quick and fair peer-review system, which is all easy to use. Visit http://www.dovepress.com/testimonials.php to read real quotes from published authors.

Submit your manuscript here: https://www.dovepress.com/nature-and-science-of-sleep-journal



