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What are the memory sources of dreaming?

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Investigators since Freud have appreciated that memories of the people, places, activities and emotions of daily life are reflected in dreams but are typically so fragmented that their predictability is nil. The mechanisms that translate such memories into dream images remain largely unknown. New research targeting relationships between dreaming, memory and the hippocampus is producing a new theory to explain how, why and when we dream of waking life events.

The night-time production of dreams is an unexplained marvel of human existence. The function of dreams and their underlying brain mechanisms continue to be matters of intense academic debate. In this article, we consider several new avenues of research that may help to overcome long-standing obstacles to explaining the functions and mechanisms of dreaming. The research concerns how episodic memories (memories of personally lived experiences) are consolidated over time and how they may be modified during dreaming (Box 1). They are altered in such a way that their autobiographical origins are obscured even though the subjective context within which they appears is a credible simulation of reality.

Memory sources are a key to dream formation

Although the concept of episodic memory was unknown to Freud, he considered such memories to be instrumental in the formation of dreams[1]. He coined the term 'day-residue' to refer to elements that connected with experiences of the previous day and that he identified in all of the dreams he scrutinized. His detailed descriptions of day-residues in his patients' dreams as well as his theoretical model describing their transformation from memories into dream elements became central to psychoanalytic theory and therapy. These elaborate 'dreamwork mechanisms' remain largely untested today.

When psychophysiological methods were introduced into the study of dreaming, the pursuit of memory sources continued with the aid of polysomnographic identification of rapid eye movement (REM) and non-REM (NREM) sleep stages and a variety of experimental methods for tracking these sources. Methods such as pre-sleep stimulation (for example, provocative films and virtual environments), sensory stimulation during sleep (for example, tones, shocks and odours) and subjects' post-hoc identification of memory sources of dream elements[2–4] demonstrated the penetrability of dreaming to experimental and naturally occurring episodic stimuli. Results confirmed the robustness of day-residue memory elements and largely attributed these elements to the fragmentation and transformation of episodic memories. More recent studies[5] suggest that dreams only rarely portray complete episodic memories, that is, reproductions of ensembles of places, actions and characters; such memories occur in a mere 1.4% of reports. Isolated fragments or features of episodic memories are more common, however. The reproduction of isolated spatial or temporal features of memories occurred in 28–38% of reports in one study[3]; 65% of dream elements were linked to features of waking events in another study[5].

In very emotional dreams such as nightmares caused by traumatic experiences, dream imagery can become highly episodic. The traumatic event may be replayed veridically as an ensemble of coherent spatio-temporal, perceptual and emotional details. It remains to be determined whether the autonoetic (or 'self-in-time') awareness of episodic memories (Box 1) is also preserved during such dreams.

If dreaming is not reliably episodic as many nightmares are, it nonetheless does simulate reality in several striking respects. Dreams seem to take place in real, spatially coherent, environments with which the self interacts perceptually, for example, by orienting, seeking and assimilating sensory information, much as it does with the real world. The self also seems to engage realistic characters in emotional and intellectual exchanges. Semantic information and a sense of knowing are often also present.

This apparent contradiction between dreaming's lack of a fully episodic structure and its portrayal of coherent virtual worlds raises several theoretical questions. Why do memories appear in dreams as fragments or partial episodes but also occasionally as complete replays? If episodic memory is inactive during REM sleep, as some researchers propose, why does REM sleep deprivation interfere with the consolidation of episodic memories in some cases but not others (see ref. 6 for a review)? Does the partial dissolution of memory episodes in dreaming imply that the basic 'units' of the episodic memory system can be identified from careful study of dream reports? Recent advances in our understanding of the memory functions of sleep (for example, see the review in this issue by Stickgold, p. 1272) are beginning to provide answers. And the study of dreaming is beginning to emerge as one of the most promising new methods for sampling the memory processes concealed beneath the veil of sleep.

The hippocampus and episodic memories in dreaming

A consensus among theorists is emerging that altered hippocampal function during sleep accounts, at least in part, for the absence of complete episodic memories during dreaming. Although they propose different mechanisms of hippocampal action (Table 1), all agree that hippocampal changes contribute to the unique characteristics of dream content. Human brain imaging findings support these speculations. Activity in the hippocampus, entorhinal cortex and other parahippocampal regions is increased during REM sleep relative to both waking and NREM sleep (see ref. 7 for a review) and is correlated with REM sleep eye movements[8]. Rhythmic slow activity (1.5–3.0 Hz) in the parahippocampal formation has also been recorded during REM sleep in human subjects[9]. There is thus ample evidence that the hippocampus is active during REM sleep even though this activity has not yet been linked specifically to changes in episodic memory organization. Just how might such a link be forged?

Three lines of inquiry are, in our view, especially pertinent to this question. Each line of inquiry addresses a particular formal characteris-

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tic of dream imagery and explores the role of the hippocampus and related structures in the production of this characteristic. Each also points to methodological improvements to the study of dream experience that might shed new light on the nature and consolidation of episodic memory during sleep or wakefulness.

The 'here' and 'now' of dream experience

The first line of inquiry concerns the fact that subjective dream experience is, for the most part, spatially and temporally coherent. Although many characterize this coherence as narrative or story-like continuity, a deeper implication is that a type of spatial and temporal binding underlies dreaming that is analogous to the perceptual binding thought to underlie waking consciousness. Dream-related binding would sustain the moment-to-moment illusion that dreaming is taking place from the first-person perspective ('here') and in the subjective present ('now'). This 'here-and-now' level of coherence would proceed in parallel with other, more global, mechanisms, such as narrative organization, and would probably operate on the threshold of subjective awareness, where it would be accessible for scrutiny by self-observational methods (for example, see ref. 10).

The role of binding disparate spatial and temporal memory elements has been attributed specifically to the hippocampus on the basis of functional magnetic resonance imaging (fMRI) studies (for example, see ref. 11). The hippocampus processes both temporal patterns (for example, temporal ordering of events and 'chunking' of events into perceptible units) and spatial patterns (for example, rapid acquisition of novel configurations and pattern completion)[12], which have been linked to the CA1, CA3 and presubiculum regions of the hippocampus. The latter contain cells that in animals seem to subserve a sense of 'place', 'head-direction' and 'direction-by-place'[12,13]. All these features could also contribute to the virtual navigation and spatio-temporal realism of dreaming. It may therefore be useful to examine whether such attributes are preserved during dreaming sequences and whether they are tied to hippocampal functioning. Animal studies already suggest that the neuronal correlates of long behavioral sequences are replayed by hippocampal neurons in real-time during REM sleep[14].

More detailed scrutiny of dream experience is clearly needed to clarify such a role for the hippocampus in maintaining the stream of perception-like imagery during sleep. Subjects could be trained to provide more accurate and detailed subjective reports of dreaming at this microstructural level. It may also be necessary to evaluate the contributions of a variety of cognitive systems and their dependence upon hippocampal activity. For example, inference processes, which are highly dependent upon the hippocampus in humans[15], may participate in resolving disparities between dream elements for which the binding process has been unsuccessful.

Studies of the dreams of patients with hippocampal damage, whose memory for recent episodic events is poor, might also shed light on the process of imagery binding. Studies are sparse, but provide a few tantalizing clues to the role of the hippocampus. Torda reports that the dreams of three such patients are infrequent but, when present, are short, stereotyped, repetitious, unemotional and lacking day-residues or symbolic elaborations[16]. In fact, they frequently replay actual events, that is, complete episodic memories. Such findings closely parallel the finding that patients with post-traumatic stress disorder suffer both diminished hippocampal capacity and episodic replay nightmares. This is consistent with the notion that an intact hippocampus is essential for access to complete episodic memories during wakefulness and dismantling of them for dream formation during sleep.

Dream sources are masked by chronobiological factors

A second line of inquiry concerns the fact that the memory sources of dreaming are often governed by temporal mechanisms that may obscure their episodic origins. Chronobiological factors at several levels seem to influence the selection of memory sources (for a review, see ref. 17). Oscillatory clocks, with a recurrent periodicity, affect both the selection of episodic memory sources (on a 90-minute REM/NREM cycle) and the selection of dream elements from recent versus remote time periods (on a circadian, early versus late-night, cycle). Interval timers, with a fixed duration, influence the selection of dream memory sources arising about 12 hours before the dream (day-residues) and those arising about a week before the dream (see ref. 18 for a review; Fig. 1). Even longer interval delays have also been observed. There is a consistent appearance of memory sources that arise from between ages 10 and 19 (ref. 4).

Some of the delayed memory elements in dreams may be explained by a widely held hippocampal model of time-limited memory consolidation[19]. It stipulates that the dependence of newly acquired memories on the hippocampus decreases over time whereas their dependence on neocortical structures, such as the medial prefrontal cortex, increases in a complementary fashion. Memories are, in a sense, relocated over time from the hippocampus to the neocortex, where they may be reiterated, for as yet unknown reasons and in qualitatively different forms, in dream content. We have demonstrated qualitative differences in the memory sources of dreams that arise from recent (day-residue) and delayed (about one-week) time periods[18].

The duration of this hippocampus-to-neocortex relocation of memories probably varies for different types or attributes of memories, extending to years in some cases[20]. But several animal studies suggest that a major transition takes place over a period of about one week (for example, see ref. 21). Hippocampal cell excitability, in particular, increases after an associative learning task (signalling neural plasticity) and then returns to baseline levels only on the seventh post-train-

Box 1 | Do episodic memories occur in dreams?

As first suggested by Tulving in 1972 (see ref. 38 for a review), episodic memories, which are remembered events experienced in the past, are distinct from semantic memories, which are items of general knowledge about the world and do not refer to any specific autobiographical context. More recently, the definition of episodic memory was expanded to include the subjective appreciation of time. It is associated with awareness, or the capacity to appreciate one's existence as extended throughout time. This 'mental time travel' is distinguished from noetic awareness, or a sense of knowing something to be true, which characterizes semantic memory. Episodic memory can also be distinguished from imagined, but non-autobiographical, virtual experiences that are realistic and appear to unfold in the apparent present, for example, fantasy and dreaming.

Researchers agree that dreaming does not express complete episodic memories. And although autonoetic awareness in dreams has not yet been examined, it is rare for subjects to report that, while dreaming, they were either aware that events arose in the past or were anticipated to occur in the future. In fact, 62.7% of all dream reports contain no temporal references whatsoever[39]. Rather, dreaming appears to mimic the flow of waking perceptual experience. Episodic fragments (characters, settings, objects) and patterns (for example, emotion sequences), as well as semantic information, undergo binding over time such that illusions of a first-person perspective and a sense of the continuous present are maintained.

Clinical and brain imaging studies link episodic memory and autonoetic awareness with activity in several prefrontal brain regions (medial, dorsolateral), visual cortex and medial temporal lobe-including hippocampus[38,40]. Hippocampal regions are especially implicated when the self-referential quality of the memory task is high[40]. Changes in brain function during REM sleep, especially increased activity in the hippocampal formation and decreased activity in prefrontal regions, are consistent with the view that altered episodic memory functioning linked to these brain regions contributes to the unique quality of dream experience.

Identification of the memory sources of dreaming is a two-step process that depends heavily on subjects' self-reflective abilities. First, subjects must accurately recall and report their dream experiences; second, they must consider individual dream contents and link them with a variety of personal memories. The recall and reporting of dreams after awakenings in the sleep laboratory is generally accepted to produce valid observations. However, subjects are usually given no training in self-observation. Their dream reports may thus lack crucial information about image formation or may unwittingly be modified to improve their narrative coherence or comprehensibility. Similarly, without training subjects may fail to identify memory sources for their dreams older than those from the past few days. Or, they may censor memory sources according to subtle demand characteristics of the experiment.

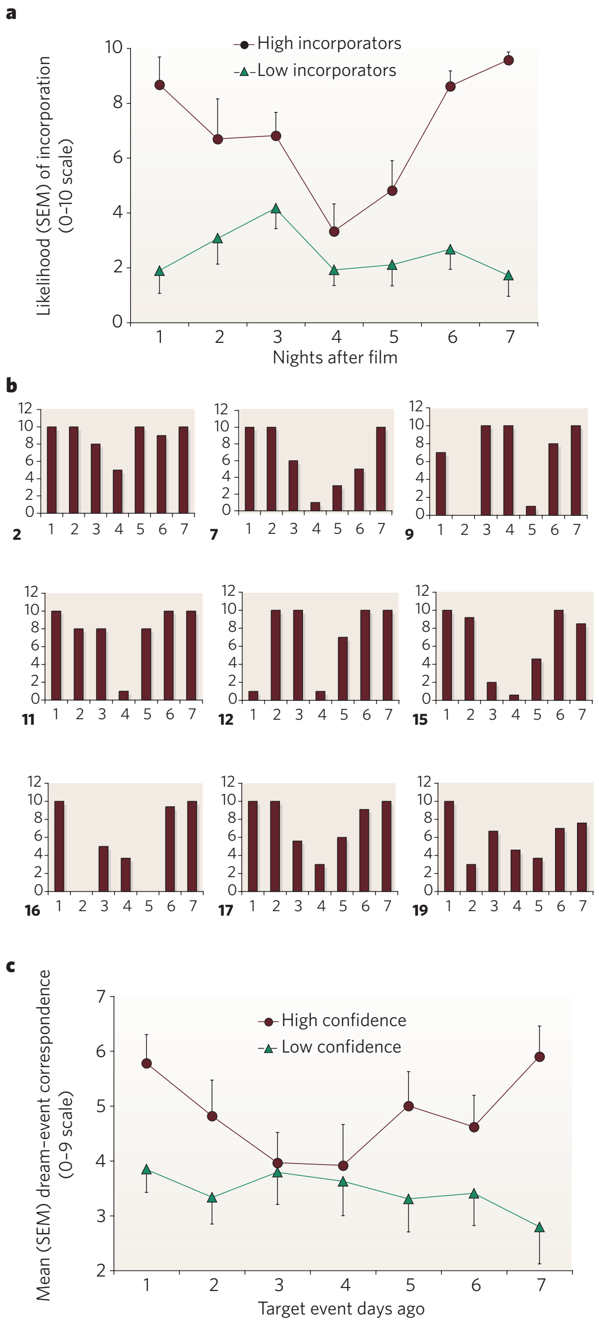

Figure 1 | Temporal variations in access to memory sources. Temporal plots of memory sources of a dramatic event shown in a film appearing in dreams conform to a U-shape. This is consistent with the notion that dreams draw upon memories at different stages of consolidation and from different regions of the brain. A decreasing gradient of access to memories of a given event across the first three nights (recent residues) may correspond to hippocampally mediated memories, whereas an increasing gradient of access to memories from days 5–7 (delayed residues) may correspond to neocortically mediated memories. **a**, Repeated measures design. Exposure to a distressing film about ceremonial sacrifice of a water buffalo produces a U-shaped curve of incorporation likelihood scores across the week for high, but not low, incorporators (data from ref. 41). **b**, Incorporation likelihood scores across the week for nine subjects in the film study who were 'high incorporators', that is, whose dreams were assigned at least one score of 10 on the 0–10 incorporation scale. The U-shaped pattern is apparent in individual subjects' scores. Empty columns indicate that no dream was recalled. **c**, Randomized between-groups design. A U-shaped curve in dream–event correspondence ratings is also observed when subjects randomized to seven different groups search for memory sources from only one of the seven days before their dream and rate their confidence in these sources as high; that is, 5 or greater on a 0–9 scale (data from ref. 18).

ing day[21]. Although no evidence links the temporal attributes of such hippocampal changes directly to delayed memory sources in dreams, three post-learning changes in REM sleep observed in animal models boost the credibility of such a link and suggest fertile avenues for further exploration. First, post-learning REM sleep time is elevated for a period of 5–7 days, as are its accompanying acetylcholine neurotransmitter levels[22]. Second, task-relevant hippocampal place-cell theta firing during REM sleep reverses polarity over a one-week period, suggesting a weakening of hippocampal synapses[23]. Last, partial REM sleep deprivation applied for 15 days after daily maze learning disrupts performance only on days 6–10 (ref. 24).

Delayed memory sources are not typically considered in evaluations of dreaming's episodic memory structure. Our group's experience with one-week-delayed sources is that subjects do not spontaneously report them and must be given specific instructions to identify them. More sophisticated methods of probing subjects' memories, including especially cued autobiographical recall and facilitated self-reflection, and of assessing subjects' confidence in their memory abilities, could be developed to further our understanding of this temporal dimension of episodic memory in relation to dream formation.

Dreams are structured by emotions

A third line of inquiry concerns the observation that in dreams emotional patterns are often preserved, structuring the contents around core relationship patterns[25] or an individual's dominant, pre-sleep emotional concerns (for a review see ref. 26).

The emotional sources of dreaming are probably regulated by the amygdala, which controls the encoding and retrieval of emotional memories and the physical expression of emotions. Amygdala activity is higher during REM sleep than during wakefulness[7] and maintains a reciprocal dependence with the hippocampus in the encoding and storage of memories. For example, hippocampal preprocessing of trace interval durations is essential for the encoding of fear memories in amygdala circuits in mice[27]. The amygdala also seems capable of gating sensory information through the entorhinal cortex to the hippocampus in rats[28]. For these reasons, further investigation of amygdalar processes in relation to the hippocampus and dreaming might help to clarify the neural underpinnings of episodic memory organization during sleep.

Surprisingly, the episodic origins of emotional structures during dreaming are often not obvious to naive subjects. Discovering such emotional sources can be a major component of the insight gained by psychotherapy clients[29]. Emotional sources may go unnoticed because they are expressed only metaphorically, possibly in the service of building adaptive new contexts to assimilate current concerns[26]. Thus, an assault victim who suffers frequently from feelings of fear mounting to panic may not notice the resemblance between such feelings and emotions felt during his recurrent nightmares of a growing storm that culminates in a tsunami and shipwreck. Elucidation of the emotional sources of dreaming may require development of methods that sensitize subjects to this subtle but influential level of dream experience while simultaneously controlling for the demand characteristics that may influence self-observation.

Conclusion

Closer scrutiny of the episodic origins of dream content are opening new research vistas on the memory functions of sleep. Although several theorists now hypothesize a role for dreaming in memory consolidation (Table 1), a causal link between dreaming and memory remains to be demonstrated. One hypothesis is that the appearance of any memory elements in dreams facilitates learning simply by reactivating those elements to their original (perception-like) state. Another is that the binding of different elements, perhaps around emotionally relevant themes, strengthens and consolidates those elements[30]. A third is that dream-related memory consolidation is regulated by oscillatory or interval timers of different frequencies, in a manner analogous to the hippocampally mediated waves of *zif-268* gene upregulation that occur during successive REM sleep episodes after

Table 1 | **Recent theories implicating altered hippocampal functioning in REM sleep to absence of complete episodic memories during dreaming**

Authors	Hypothesized mechanism	Consequence for dream formation	Possible function
Stickgold, Hobson, Fosse & Fosse[35]	In REM sleep, reduced information flow from hippocampus to neocortex; flow of weakly associated semantic contents from neocortex to hippocampus	Illogical sequences of barely related objects, characters and locations lacking spatio-temporal coherence	Selective strengthening of associations and consolidation of semantic memories
Johnson[36]	Predominance of theta activity during REM sleep causes neocortex to present incongruous and unpredictable information to hippocampus	'Context memories': composites of elements merged from many separate episodic experiences	Context enables retrieval of episodic memories during other ('non-theta' mode) states, for example, waking
Payne & Nadel[37]	Increasing cortisol late in sleep diminishes hippocampal-to-neocortical communication; activates memory fragments without spatio-temporal contexts afforded by hippocampus	Fragmented, bizarre imagery synthesized and 'smoothed' into narrative themes	Strengthening, integration and maintenance of memories
Paller & Voss[30]	Sleep strengthens connections among dispersed cortical networks and hippocampal–neocortical connections	Narrative created from fragmentary information	Declarative memories consolidated adaptively, that is, in relation to problems, goals, recent experiences

the induction of long-term potentiation in awake rats[31].

A final, more widely recognized, hypothesis is that dreaming about newly learned material enhances subsequent recall of that material. Three studies in human subjects support this hypothesis and suggest methodological avenues for future exploration. The first is that interrelated dream elements are better recalled in a surprise morning recall task than are unrelated elements[32]. The second is that pre-sleep stories are better recalled in the morning when subjects dream frequently about constituents of the stories[33]. The third is that completion of a mirror-tracing task leads to reports of dreams that metaphorically represent the task (for example, 'trying to stay on a road')[34].

A continuing obstacle to proving whether dreaming plays a causal role in memory consolidation is the difficulty subjects encounter in identifying the source memories of their dreams. Even though the assessment of feature binding, temporal factors and emotional structures all suggest novel methods for eliciting and assessing subject reports, future progress may ultimately depend upon whether subjects can be taught to identify and report the non-obvious minutiae of their dreams and memories with sufficient accuracy that the dreamwork mechanisms connecting the two can be discerned. In an era of high-resolution brain imaging, similarly high-resolution reports of dream imagery may be needed. To achieve this, the method of self-observation preferred by Freud, William James and others may yet prove to be among the most productive — particularly in a domain for which the object of study remains directly observable only by dreamers themselves. ■

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