

# Are life episodes replayed during dreaming?

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**New phenomenological data demonstrate that integrated life episodes are incorporated in no more than 1–2% of dream reports. This appears to be at odds with the replay of temporally sequenced memory at the level of neuronal ensembles observed in some animals during sleep. This result will constrain emerging ideas on memory reactivation during sleep and the role of sleep in memory consolidation.**

Yesterday, on your way home you met an old friend and invited him/her for dinner at your place on Sunday night. This morning, you remember that you have dreamt of this friend over night. The presence of this friend in your dream is nothing exceptional, because it is well established that more than half of spontaneous dream reports include clearly recognizable waking elements [1–3]. But did your dream reproduce exactly what happened when you met your friend yesterday? Are dream experiences perfect imitations of life events? In a recent article, Magdalena Fosse *et al.* [4] addressed this question by analyzing the degree of similarity between descriptions of waking activities and dreams reported the next morning. They found that dreams do not reproduce real-life events. The authors concluded that sleep has no role in episodic memory consolidation. This counterintuitive result might nonetheless contribute to a better understanding of memory processing across the circadian cycle.

Fosse *et al.*'s surprising discovery can be best understood if we consider both the nature of the material analyzed and the operational definition of episodic memory used in this study. Over a period of 14 days, 29 subjects wrote down all recalled dreams and scored the dreams for incorporation of any waking experience. The subjects also kept a log of daytime activities, events, and concerns to allow a later independent third-person rating of the incorporation of episodic memories. From the total of 299 dream reports, 194 reports (65%) contained 364 memory entries (i.e. material from past experience). Incorporation of episodic or narrative events from the subject's recent life was then assessed by a stepwise procedure (Fig. 1). For a dream memory entry to be an episodic-memory candidate, it had to meet the following criteria: first, it had to be confidently associated with a waking event by the subjects, and share with the real-life event the same location plus two additional features. These additional features could be characters, objects, actions, themes or emotions. Second, the memory source

had to be an actual perceived event (not just a thought), and the corresponding dream report had to include all objects, actions or characters that were present in the original waking event. The validity of the coding performed by the subjects themselves was finally confirmed by five external judges. At the end of these selective steps, only five strong candidates for episodic memory replay were found in the original 299 dream reports and represented only 1.4% of all memory entries.

## The memory-replay hypothesis

To understand the implications of this paper, it is useful to place it in the context of other related studies. Several studies have examined the beneficial effects of sleep (or the detrimental effects of sleep deprivation) on subsequent behavioral performance on trained tasks [5–8] and on learning-related neural changes [9]. In addition, several studies have investigated memory reprocessing *during* sleep [10–13]. Converging evidence has accumulated to suggest that some waking experiences might be replayed during sleep. Such experience-dependent reactivations have been observed in both humans and animals. At the

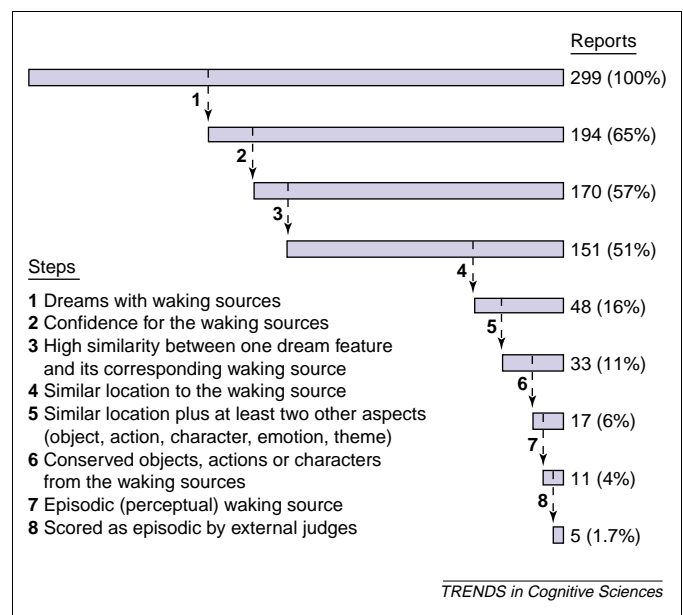


Fig. 1. Stepwise selection of episodic memories. From top to bottom: initially confidently rated memory elements are progressively excluded if they do not fulfill the requirements for episodic memory. For example, the criterion 'Similar location to the waking source' (Step 4) excludes more than two-thirds of the episodic memory candidates. The one-third of memory entries referring to waking thoughts are similarly dropped because they do not correspond to actual perceptions (Step 7). Adapted from [4].

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cellular and neural-network levels, hippocampal cells in the rat can reproduce temporally sequenced patterns of activity during NREM (non-rapid-eye-movement) and REM sleep, reflecting tens of seconds to minutes of behavioral pre-sleep experience [10–12]. These cell-recording data suggest that rats were cerebrally rehearsing their travel in the maze from the start location to the food location while asleep. This replay might relate to the role of the hippocampus in the formation and long-term consolidation of episodic, temporally structured memories. These hippocampal-dependent spatial memory tasks represent a good animal model for human spatial episodic memory [14]. Yet, there is still an explanatory gap between the activity of hippocampal neuronal ensembles observed in rodents and the phenomenological account of episodic memory retrieval in humans. At the macroscopic system level, a recent neuroimaging study has revealed experience-dependent reactivation of distributed cerebral regions during REM sleep in humans [13]. Several brain areas activated during the execution of a serial-reaction-time task during wakefulness were significantly more active during REM sleep in subjects previously trained on the task than in non-trained subjects. These results support the hypothesis that memory traces are processed during REM sleep in humans.

At the behavioral or cognitive level, the immediate phenomenological correlates of memory reprocessing in sleep are almost totally obscure. How can such nocturnal reactivation of waking experiences be investigated? On the assumption that the formal properties of dreams reflect the quality of underlying memory reprocessing during sleep and dreams, Fosse *et al.* have undertaken the first phenomenological assessment of episodic replay during human sleep. As mentioned above, their study indicates that dreams are not directly generated by the reactivation of integrated episodic waking experiences. Yet, many of us will vividly remember examination dreams from their university years, skiing dreams from holidays in the mountains, dating dreams during a love affair, even computing dreams for those who are skilled programmers. How can these observations be reconciled?

When studying the role of sleep in memory reorganization and consolidation, one should keep in mind that memory is not a unitary phenomenon [15]. Long-term memories are likely to involve multiple memory systems, such as declarative (i.e. explicit, semantic or episodic) and non-declarative (i.e. implicit, procedural) memory. These systems rely on distinct neuroanatomical structures and are implicated in the learning, consolidation or storage of different kinds of knowledge and skills [16,17]. With this perspective in mind, the Fosse *et al.* study focused only on those neurocognitive events occurring during sleep that are accessible to declarative memory, and perhaps expressed in dream reports as the replay of coherent waking episodes.

#### Functional dissociations in the sleeping brain

Fosse *et al.* found that all the 297 *confidently identified* memory entries came from a subset of 170 dreams. This means that 65% of the dreams contained on average two specific features from the waking life of the subjects.

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Incorporation of such specific experiential elements from waking life in dreams is a well documented fact [18–20]. In light of the new findings of an absence of replay of whole integrated episodic events, we still have to understand why isolated episodic elements do appear in dreams.

Two-stage models of long-term memory formation can provide a possible explanation [21,22]. During active waking, information flows into the hippocampus where an intermediate-term representation is formed by binding together different elements of an episodic memory. During slow-wave sleep, memory traces in the hippocampus are consolidated and transferred to the cortex through discrete neuronal bursts, rather than continuously [21]. However, during REM sleep, as Fosse *et al.* emphasized, hippocampal outflow to the cortex is blocked, internally generated information flowing mainly from the cortex to the hippocampus. The hippocampus constitutes the major associative organizer in the human brain in the context of episodic memory retrieval. Because the information (as far as recent memories are concerned) probably flows from independent cortical modules towards the hippocampus during REM sleep, there is no reason to expect the report of complete episodic memories in REM sleep. This would be different for older consolidated memories, which are essentially coded within interconnected cortical networks. Furthermore, whereas controlled memory recall in the waking state depends on influences from frontal control systems, during sleep the dorsolateral prefrontal cortex is strongly deactivated [23,24]. Taken together, these observations would predict that episodic elements will be reactivated in a fragmented fashion during sleep, rather than in the form of an integrated life episode.

#### A partial role for memory consolidation?

Perhaps the toughest conundrum is to figure out why the authors concluded that sleep has no role in episodic memory consolidation when 65% of the reports contained vivid waking events. On the basis of the currently available data on memory consolidation during sleep, one might be inclined to postulate that the replay of isolated elements (extracted from their original context) is likely to be important for the integration of new features into existing cognitive representations held within functionally specialized brain areas. Furthermore, experience-dependent patterns of cerebral activity observed during human sleep might be associated with re-enacting only relevant or novel features that need selective reprocessing within these brain areas, while other characteristics of the original waking experience can be disregarded [25]. After meeting a new friend in an Italian restaurant, for example, we might dream of a sailing adventure with this person in the Mediterranean. Seeing this new friend's face in our dream might then provide a phenomenal correlate for some reactivation during sleep of new traces in face processing modules of the brain. Further dream research using a neurocognitive approach will eventually show whether or not this hypothesis is correct.

#### Dreams are like thoughts: towards a new heuristic

Importantly, the stepwise coding procedure used by Fosse *et al.* revealed that a significant proportion of memories in

dreams referred to waking thoughts rather than to actual perceptions, representing one-third of the final episodic candidates scored by the subjects. These were not included, however, as episodic memory candidates (Step 7 in Fig. 1). This is because our incessant thoughts, explicit expectancies, and other mental representations do not fit the conventional definition of life episodes. Is this restrictive definition really justified? In particular, the high frequency of remembered mental activities as opposed to events brings to question whether thoughts should be in fact considered as part of life episodes. This point stresses the need for a more articulated account of waking experiences. Whilst future dream studies will require a new appraisal of the information actually extracted and processed by our brains when awake, it is also clear that dreams exhibit functional dissociations that might help to identify the neurocognitive constituents of waking experience and of memory [25].

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#### Research Focus Response

## Response to Schwartz: Dreaming and episodic memory

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In Schwartz's review [1] of our recent paper on episodic memory replay in dreams [2], Schwartz asks 'why the authors concluded that sleep has no role in episodic memory consolidation', pointing out that 'when studying the role of sleep in memory reorganization and consolidation, one should keep in mind that memory is not a unitary

phenomenon'. We fully agree with Schwartz on this latter issue and clarify our view on the former.

Central to the question of episodic memory consolidation in sleep is the hippocampus formation and the entorhinal cortex. This system plays a critical role in both the encoding and retrieval of recent episodes and events [3,4]. During episodic recall, information is typically thought to flow from the hippocampus into the cortex via the parahippocampal region [5].

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