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## Parsing the role of sleep in memory processing

Robert Stickgold

It would be nice if we could talk about sleep and memory as if there were only one type of memory and one type of sleep. But this is far from the case. Sleep and memory each comes in many forms, and furthermore, memories can go through multiple forms of post-encoding processing that must be individually addressed. Finally, sleep stages *per se* do not affect memories. Rather, the neuromodulatory and electrophysiological events that characterize these sleep stages must mediate sleep-dependent memory processing. In this review, we attempt to parse out the relative contributions and interactions of these often frustratingly complex systems.

### Addresses

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### Parsing off-line memory processing

Three separate issues must be addressed in discussing how memories are processed after their initial encoding; first, the type of memory; second, the type of processing; and third, the time course of the processing. [Figure 1a](#) shows the standard taxonomy of human memory [1]. While originally based on conceptual differences among memories, these categories are largely subserved by distinct anatomical brain regions. Thus, declarative memories are hippocampally dependent [2], at least initially (e.g. [3]), while procedural memories are hippocampally independent, instead relying heavily on the striatum [4,5].

Less clear is the extent of post-encoding memory processing ([Figure 1b](#)). That some form of post-encoding processing occurs has been clear since the work of Müller and Pilzecker in 1900 [6], who introduced the concept of memory ‘consolidation’ as a form of post-encoding memory processing that turned an initially labile memory into a permanent form. These findings led to a dichotomization of memories. There was an initial, labile form of

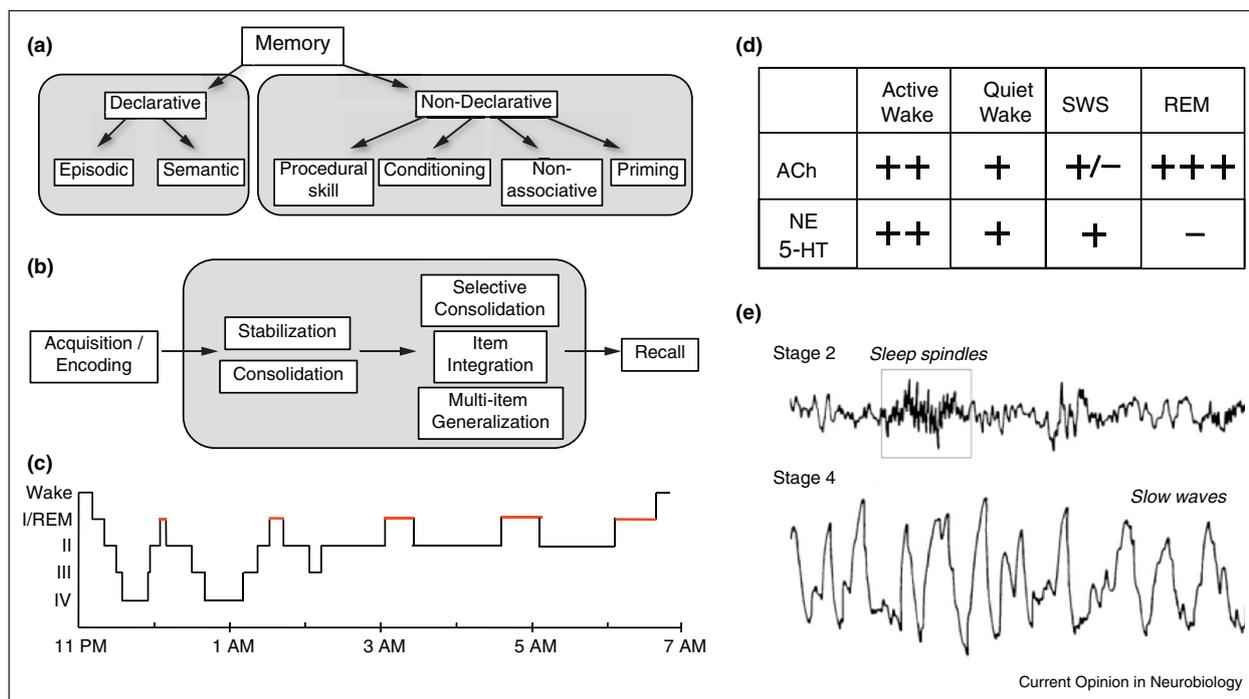
memory that could be disrupted by electroconvulsive shock or protein synthesis inhibitors, and a consolidated form, into which the labile form was normally converted within a matter of hours [7]. But even these supposedly permanent memories could often be disrupted by hippocampal lesions after even longer post-encoding intervals—up to 2–5 days in rats [8], 4–8 weeks in primates [9] and years, perhaps even decades, in humans [10].

Beyond consolidation, several additional forms of post-encoding memory processing can take place. These can result in absolute improvements in procedural task performance, or qualitative changes in declarative memories. These will be discussed more fully below, as they are often sleep-dependent changes. But they include selective item consolidation, where only some studied items are selected for retention; item integration, where new memories are integrated into preexisting networks of associated memories; and multi-item generalizations, where gist and rules are extracted from a set of newly formed memories, and where false memories can be generated.

All of these modifications of an initially encoded memory occur over time. Some forms are complete within 2–4 hours, while others may extend across the life of the organism. Recognition of the full sweep of this time course makes the term ‘consolidation’ feel inadequate, certainly for describing the sum of these processes, and perhaps even for describing the initial ‘consolidation’ described by Müller and Pilzecker [6] and those who followed. Indeed, the permanence of these consolidated memories has been shown to be a misnomer. ‘Consolidated’ memories can be returned to a labile state simply by reactivating them. Once relabilized, they must be ‘reconsolidated’ by a process that requires protein synthesis [11], and in the absence of such reconsolidation, the memory can be lost. Thus, memory consolidation may only hold a memory from the time of its consolidation until it is next recalled, when consolidation must occur anew.

We have begun to refer to this collection of post-encoding processes as memory ‘evolution’ [12\*\*]. We use this term to highlight two aspects of post-encoding processing. First, the changes that occur over time shape the memory into a form that can be quite different from its original form, but which has evolved into a form that optimally serves the projected future needs of the organism. Thus, some memories are most useful if kept distinct from others and in their original form, while others are most useful when combined with others and subsumed under

Figure 1



Sleep and memory. Sleep-dependent memory processing depends on **(a)** the type of memory being processed, **(b)** the stage or form of processing, **(c)** the sleep stage in which processing occurs, **(d)** the neuromodulatory regulation of that sleep stage, and **(e)** the unique electrophysiological activities found in specific sleep stages.

an overarching rule that succinctly describes all of the original memories. The second reason we use the term evolution is to highlight the fact that memories continue to change over time, molded by new experiences and new needs.

### Parsing the forms of memory processing

Any discussion of sleep and memory requires that we understand what types of memories and memory processes are under consideration. But the state dependency of these processes can be summarized by stating that, with the exception of the rapid (2–4 hours) consolidation that provides the initial stabilization of the memory, there is evidence that each of these forms of memory processing occurs preferentially, if not exclusively, during sleep.

### Memory stabilization and enhancement

While the initial consolidation of memories occurs independent of sleep–wake states, sleep can produce additional stabilization and even absolute enhancement. For declarative memories, subjects who memorize a list of word pairs are more susceptible to interference from subsequently learned related word pairs if the interference training comes after a day of wakefulness than if it comes after a night of sleep [13,14]. Enhanced memory following sleep, relative to wake, has also been seen for

word pairs [15], as well as for the details within stories [16] and even nonsense syllables [17]. But in these studies, what is seen is *less memory deterioration* across sleep than across wake, rather than an absolute improvement in memory after sleep. Such absolute improvement has only been seen for procedural learning, where competing processes of forgetting are often not present. Such absolute improvement following sleep, but not following daytime wake, has been seen for motor [18,19], visual [20] and auditory [21] learning tasks, as well as more complex procedural learning tasks, such as the Tower of Hanoi [22] or the probabilistic weather prediction task [23]. The absence of absolute performance enhancement for declarative memories suggests that there is forgetting of these memories across both wake and sleep that exceeds any enhancements of memory during sleep.

### Selective item consolidation

More recently, it has become clear that not all memories benefit from sleep. In some cases, this has been seen as the selective retention of emotional material over neutral, whether pictures [24], emotional texts [25], or simply emotional portions of pictures [26]. In other cases, sleep selectively benefits newly formed memories that are expected to have future relevance [27\*] or for which subsequent recall will be rewarded [28], even when these

factors are introduced only after learning is complete. Whether these truly represent different selection criteria remains unclear. For example, future relevance and reward can affect the emotional salience of a memory, while subjects may perceive emotional and rewarded memories as more future-relevant than unemotional and unrewarded material. Studies designed to distinguish among these possibilities — for example tests of sleep's impact on emotional memories that subjects do not expect to be tested on — are yet to be reported.

### Item integration

In our discussions so far, we have portrayed sleep's role as simply stabilizing and strengthening memories. Conceptually, this can be imagined as a process that simply stabilizes and strengthens all of the synapses that contribute to the originally encoded memory. But there are other forms of memory processing, and specifically of sleep-dependent memory processing, that cannot be explained simply by such synaptic level consolidation. Such systems level processing can be seen when newly formed memories are integrated into older semantic networks. One example of this is *lexical integration*, seen, for example, when a subject learns a new word like 'CATHEDRUKÉ' that is similar to a well-known word, in this case 'CATHEDRAL'. Learning such words can hinder the recognition of the similar word, so that recognition, in this case, of CATHEDRAL is slowed. But this effect only develops some time after the new word is learned, and reflects the word's integration into the subject's mental lexicon. Sleep's role in the process is unclear; a first study reported that integration was only seen after sleep [29], although a repetition study found integration both after wake and sleep. In this second study, however, incorporation over sleep correlated with sleep spindle activity [30], suggesting an active, sleep-dependent process of lexical integration.

### Multi-item generalizations: gist and rules, false memories and insights

Perhaps the most powerful forms of off-line memory processing, for which sleep again gives a distinct advantage, involve multi-item generalizations. While item integration incorporates a single newly learned item into a preexisting schema, multi-item generalization involves the incorporation of a number of newly encoded memories into a new schema. Such new schemas can take several forms (Figure 2). For example, when subjects are asked to remember several lists of words, each of which contains words strongly related to some central gist word not included (e.g., DREAM, REST, BED, TIRED, AWAKE, but not SLEEP), subjects normally identify the gist word, but then often believe that it was part of the list [31,32]. While such gist extraction occurs during the initial encoding of the studied words, a night of sleep, but not a day of wake, leads to a selective retention of the false memories for these gist words, while the actual studied

words are forgotten [26], resulting in a memory that is less accurate but arguably more useful.

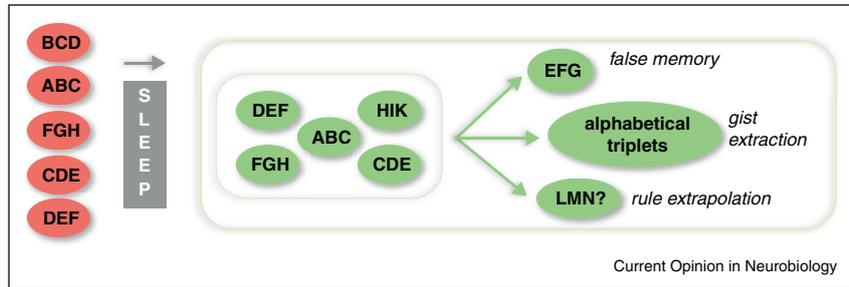
In other cases, sleep helps extract the rules that control the relationship between learned items. An example of this is the *transitive inference* task. Subjects study five pairs of Faberge egg-like figures, and learn to choose one over another in the pairings shown at the top of Figure 3, where the symbol ' $\Rightarrow$ ' indicates the subjects learn, in the case of  $A \Rightarrow B$ , to choose A over B. By learning the pairs  $A \Rightarrow B$ ,  $B \Rightarrow C$ ,  $C \Rightarrow D$ ,  $D \Rightarrow E$ , and  $E \Rightarrow F$ , subjects also implicitly learn a transitive pattern, ' $A \Rightarrow B \Rightarrow C \Rightarrow D \Rightarrow E \Rightarrow F$ '. Knowledge of this inferred pattern can be tested by showing subjects new pairs, never seen before, whose relationships can be inferred from the larger pattern. Thus, the pairs B–D and C–E (Figure 3, middle row) have the implied relationships  $B \Rightarrow D$  (from  $B \Rightarrow C$ ,  $C \Rightarrow D$ ) and  $C \Rightarrow E$  (from  $C \Rightarrow D$ ,  $D \Rightarrow E$ ). These are first order inferences, made by combining two learned relationships. Similarly, the second order inference,  $B \Rightarrow E$  (Figure 3, bottom) is inferred by combining three learned relationships ( $B \Rightarrow C$ ,  $C \Rightarrow D$ ,  $D \Rightarrow E$ ).

As with the integration of new words, like CATHEDRUKÉ, into one's mental lexicon, effective knowledge of these first and second order transitive inferences is not seen immediately after the five training pairs have been learned [33]. After 12 hours of daytime wake, subjects show some knowledge for both the first and second order inferences, choosing the correct figures 74% and 70% of the time, respectively. After 12 hours including a night of sleep, they choose the correct first order inference figures 72% of the time, similar to that seen after an equivalent period of wake. But they now identify the correct second order inference 93% of the time, making 4–5 times fewer errors (7% vs. 30%), and significantly fewer than after the period of wake. Thus the sleeping brain is able to generalize the learned relationships in individual item memories more effectively than the wake brain.

### Parsing the sleep-stage dependency of memory processes

The examples described in the previous section just hint at the depth and breadth of research demonstrating sleep-dependent memory processing. With the multiplicity of memory systems and of forms of memory processing, one inevitably asks how these relate to the various sleep stages (Figure 1c) and, more deeply, with the various neuromodulatory (Figure 1d) and physiological features of these stages. Indeed, numerous relationships have been proposed. As far back as 1974, Greenberg and Pearlman proposed that the learning of novel information occurred during REM sleep, while information easily linked to existing information was processed during nonREM (NREM) sleep [34]. More recent models include the

Figure 2

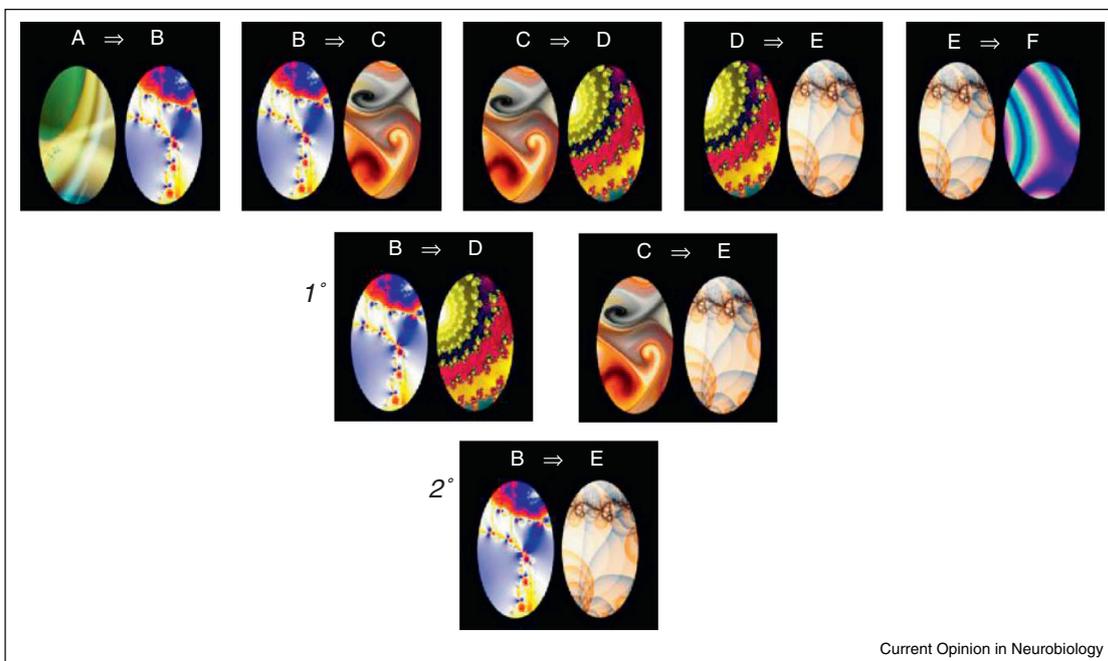


Multi-item memory processing. When several related item memories are formed in a brief period of time, sleep can process the memories both individually and as a group. Multi-item processing during sleep can extract a gist representation of the entire set of memories, extrapolate a general rule defining the nature of individual items, and even generate false memories from the gist or rules formulated by the sleeping brain. From Ref. [12\*\*].

suggestion that slow wave sleep (SWS), which makes up the deeper stages of NREM sleep, processes declarative memory, while REM sleep processes procedural memory [35], that SWS carries out synaptic level consolidation while REM performs systems level processing [36], and the opposite [37\*\*]. In short, no model for the sleep-stage dependencies of memory processing has been found to adequately explain the existing data.

Nor do physiological markers of different sleep stages (Figure 1e) explain these observations of sleep-dependent memory processing. While sleep spindles (11–15 Hz) [38–40], slow wave activity (1–4 Hz) [19,41,42] and slow oscillations (<1 Hz) [43] have all been implicated in sleep-dependent processing for specific memory tasks, clear and consistent correlations between any of these and specific categories of memories or memory processes are lacking.

Figure 3



Transitive inference. When subjects learn the relationships between a series of items, generalization can include the inferring of a transitive relationship among the items. Thus, if taught to select item A over B, item B over C, item C over D, etc., they will infer by transitivity that they should select A over C and B over E. Sleep selectively enhance the more distant transitive assumptions (bottom row). Such inferences of transitivity need not be correct. In the game rock-scissors-paper, one selects rock over scissors and scissors over paper, but paper over rock. From Ref. [13].

### Parsing the role of wake in sleep-dependent memory processing

Some forms of memory processing clearly occur during wake. These include aspects of motor memory [44], as well as the examples of lexical integration [30<sup>\*</sup>] and transitive inference [33] discussed above. In all cases, however, further processing occur during subsequent sleep [18,30<sup>\*</sup>,33]. How processing in wake and sleep are related remains a topic of active investigation. While some aspects of wake processing may be totally independent of subsequent sleep-dependent processing, evidence suggests that other aspects may play a role in identifying which memories will be subsequently processed during sleep. Brain fMRI studies have shown that patterns of activity seen during learning are recapitulated during subsequent wake, both during quiet rest [45<sup>\*\*</sup>] and during performance of a different task [46]. In the case of quiet wake, fMRI activity was shown to predict subsequent task performance [45<sup>\*\*</sup>]. Neither of these studies indicate that this activity is preparatory for subsequent sleep-dependent processing, but unpublished results from our laboratory suggest that brain activity during post-training rest, whether measured by fMRI or high density EEG, can predict subsequent sleep-dependent task improvement. These findings obviously need further evaluation, repetition, and extension before anything firm can be said about them. Nevertheless, the question of whether memories are 'tagged' during wake for subsequent processing during sleep [12<sup>\*\*</sup>] or are only selected during sleep, remains unanswered question.

### Parsing the contribution of circadian rhythms

A recurring concern in studies of sleep and memory is the possibility of circadian confounds [47,48]. Most simply stated, the finding that memory is improved across a night of sleep but not over an equal period of daytime wake cannot distinguish models of sleep-dependent memory consolidation from models involving circadian fluctuations in performance. If individuals simply perform better in the morning than in the evening, one would see a *decrease* in performance across daytime wake and an *increase* across a night of sleep without any real changes in memory. Several methods have been used to demonstrate that the effects indeed involve sleep-dependent changes in memories.

### Sleep deprivation

Studies have trained and tested subjects at fixed times, with groups differing in terms of whether sleep is allowed the night after training. Of course, testing subjects after a night of sleep deprivation introduces its own confounds, but several studies have delayed retesting until after one [49] or two [20] nights of recovery sleep, and all have shown poorer performance when subjects were sleep-deprived after training. Thus, since there were no circadian differences between groups, it was the presence or

absence of sleep during the post-training night that led to improved performance.

### Nap studies

Other studies have trained and tested subjects at fixed time during a single day, with groups differing in terms of whether a nap is allowed between training and test. Again, the nap groups consistently show better performance than those who maintained normal wakefulness during the afternoon [40,50–53]. With an absence in circadian differences, the memory effect must be due to the nap.

### Immediate testing

Another approach is to compare baseline performance at different times, as well as to use control groups tested shortly after training. This is done when groups are trained and tested at different circadian times, such as when one group is trained in the morning and tested in the evening and another is trained in the evening and tested the next morning. By comparing performance during training, one can determine whether there is any circadian influence on training. Then, by training control groups either in the morning or evening and testing them 10–30 min later, one can determine whether there is any circadian influence on testing. Several studies have followed such protocols and found overnight improvement in the absence of any measurable circadian influences [18,26,54].

### Sleep stage correlations

A final argument against major circadian influences are studies that demonstrate that sleep stage or physiological markers of sleep correlate with overnight improvement. Since all subjects in these studies are trained and tested at the same times, the correlations with sleep attributes cannot be due to varying circadian influences, but instead must reflect differences in sleep physiology.

### Altered circadian rhythms

Another approach, which has not been attempted to date, is to study these effects in subjects kept in constant illumination, without time cues, or running on a modified 20-hour day. Such interventions result in a temporal disjunction between the circadian and sleep cycles, and would allow a cleaner characterization of the effects of sleep and circadian rhythms. Practically, this would require piggybacking a memory study onto an ongoing study of circadian rhythms, as the cost per subject is 10–100 times higher than for a simpler sleep and memory study. To our knowledge, no such studies have been carried out.

While it can be argued that none of these approaches by itself is an adequate argument against circadian influences, together they provide a very strong argument that

the major effects seen in these studies are, indeed, due to sleep-dependent memory processing.

## Conclusion

The last decade has provide a wealth of information documenting first the existence and then the extent of sleep-dependent memory processing. As it always happens when new fields of research are opened, these initial successes have unearthed immense areas of uncertainty and ignorance that require further investigation. But the shape of these questions has become much clearer, as have the rewards that will follow their resolution. Indeed, the study of sleep and memory has moved from an ancillary role to a position at the cutting edge of memory research.

## Acknowledgement

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