

1 **Memory reactivations during sleep: a neural basis of dream**
2 **experiences?**

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13

14 **Keywords (2 to 6)**

15 Dreaming, memory reactivation, neural replay, sleep, memory consolidation

16 **Abstract**

17 Newly encoded memory traces are spontaneously reactivated during sleep. Since their
18 discovery in the 1990s, these memory reactivations have been discussed as a potential
19 neural basis for dream experiences. New results from animal and human research, as
20 well as the rapidly growing field of sleep and dream engineering, provide essential
21 insights into this question, revealing both strong parallels and disparities between the two
22 phenomena. We suggest that while memory reactivations may contribute to subjective
23 experiences across different states of consciousness, they are not likely to be
24 experienced directly as dreams. We identify important limitations in current research
25 paradigms and suggest novel strategies to address this question empirically.

26 **Are memory reactivations experienced as dreams?**

27 Several decades of research show that sleep plays an important role in memory
28 consolidation, the process by which short-term memory is strengthened and integrated
29 into long-term memory networks. **Memory reactivations** (see Glossary), whereby newly
30 formed memory traces become spontaneously active again after encoding, have been
31 proposed as one mechanism for memory consolidation during sleep in the **active system**
32 **consolidation** model [1-5]. It has been suggested that dreaming could be the conscious
33 manifestation of these memory reactivations during sleep (e.g., [6, 7]). However, most of
34 our knowledge of memory reactivation is based on rodent studies, limiting the ability to
35 compare them to the human experience of dreaming. Recent advances in brain imaging
36 have provided evidence of similar reactivation processes in humans. Together with novel
37 findings in rodent research and recent studies examining dreaming and memory
38 consolidation, we are now able to compare memory reactivations and dreaming on key
39 aspects to discuss similarities as well as differences (Figure 1, Key Figure).

40 **Memory reactivations: pioneering work in rodents**

41 The first empirical evidence for memory reactivations during sleep came from studies that
42 recorded the hippocampus of rodents during spatial exploration of a maze and showed
43 that cells from places that were co-active during exploration had correlated activity
44 patterns during subsequent periods of **non-rapid eye movement (NREM) sleep** [8] and
45 that the temporal order of the original sequence during wakefulness was partially
46 preserved during sleep (referred to as '**neural replay**') [9]. Since then, a growing number
47 of studies corroborated the occurrence of hippocampal memory reactivations in a variety
48 of species, both during sleep (e.g., [10-17]) and quiet rest (e.g., [18]). Memory
49 reactivations have been closely tied to **sharp wave-ripple (SWRs)** activity arising from
50 the hippocampus [19] but have also been recorded across a wide range of brain regions
51 (e.g., [20, 21]). A direct role of memory reactivations in memory consolidation is
52 suggested by their association with improved post-sleep performance (e.g., [22, 23]) and
53 by the fact that their suppression (e.g., by disrupting SWRs after learning) impairs
54 memory performance (e.g., [24-26]).

55 **Capturing memory reactivations in humans**

56 For a long time, evidence of memory reactivations in humans was limited to neuroimaging
57 studies showing that broad patterns of brain activity produced by an experience were
58 repeated during subsequent sleep. Reactivations occurring in both NREM sleep [27] and
59 **rapid eye movement (REM) sleep** [28, 29] showed an association with improved
60 learning. In the last five years, studies using intracranial electroencephalography (EEG)
61 recordings in epileptic [30, 31] and quadriplegic [32, 33] patients have shown the first
62 direct evidence of neural reactivations in humans. Additionally, advances in multivariate
63 pattern analysis made it possible to capture spontaneous reactivations of specific
64 memories using high-density EEG [34, 35] or simultaneous EEG and fMRI recordings [36]
65 and to link them to increased memory performance.

66 **Memories are incorporated into dreams**

67 The fact that memories are reactivated during human sleep has fueled discussion on
68 whether reactivation processes could be subjectively experienced as dreams. The idea
69 that dreams play a role in memory processes at night has long been suggested [37, 38].
70 Over 80% of dreams contain identifiable memory sources [39-41], but whether these
71 memory “incorporations” reflect neural reactivations is still unknown. Several studies have
72 investigated whether incorporating memory elements into dreams is associated with
73 better retention of those memories. This would suggest that dreams are either relevant
74 for or a direct reflection of memory consolidation during sleep. Wamsley et al. [42, 43]
75 showed that following the exploration of a virtual maze, participants who incorporated
76 elements of the task into their dreams exhibited larger improvements than participants
77 who did not incorporate the task into their dreams. In contrast, thinking about the task
78 spontaneously while awake did not predict performance. Other studies have shown
79 similar effects (e.g., [44-47]). Specifically, NREM dream incorporations were associated
80 with declarative memory performance [46], whereas REM dream incorporations were
81 associated with procedural memory performance [47]. However, task incorporation rates
82 are often low, and not all studies find an effect of dream incorporation on memory
83 performance (e.g., [48-50]); thus, the role of dreaming in memory consolidation remains
84 unclear.

85 Here, we will compare memory reactivations and dreaming on several key points,
86 covering 1) *what* type of memories are reactivated; 2) *when* they occur; 3) *how* they are
87 reactivated; and 4) their respective neural correlates at the macro- and microstructure
88 levels (see Table 1 for a summary).

89 **What is being reactivated?**

90 ***Content of reactivation***

91 Memory reactivations in sleep were first and foremost studied with spatial tasks in rodents
92 (e.g., running a linear track). Therefore, most of our knowledge of reactivation processes
93 is based on spatial content [19]. Nonetheless, a few recent investigations in both humans
94 and non-human mammals have extended evidence of reactivation for other types of
95 experiences, such as motor learning (e.g., [32, 33, 51]), visual memory [31], associative
96 memory [34], declarative memory [35, 36], and social memory [52]. However, which
97 information of the encoded memory is reactivated remains unclear [53]. The content of
98 reactivation may not only reflect past learned experiences but also anticipated
99 experiences. The activation of neural patterns simulating new experiences (i.e., novel
100 trajectories based on previous experiences that are spatially plausible, but have not been
101 explored during wake) was recorded during wake [54] as well as during sleep [55]. These
102 ‘imaginary’ reactivations could reflect the exploration of anticipated situations or the
103 maintenance of cognitive maps [54]. Interestingly, other studies have suggested that **pre-**
104 **play** (i.e., activating the cell-sequence scaffold that will be used to encode new spatial
105 experiences) also happens during sleep before exploration [56].

106 In contrast with memory reactivations, spatial content in dreams has rarely been studied.
107 Nonetheless, the projection of a dream-self in space is a common structuring mechanism
108 of dream experience [57]. Wayfinding behaviors, where the dreamer explores the dream
109 environment, are common in dreams collected in the laboratory [58] and participants
110 dream about mazes or other exploratory behavior after being tested on virtual maze tasks
111 [42-44]. However, dream locations and environments are often vague and discontinuous
112 [59]. Dreams also incorporate a variety of non-spatial experiences, with the construction
113 of complex oneiric worlds based on social, emotional, cognitive, and perceptual

114 experiences from both the recent and the distant past. Experimentally induced
115 incorporations into dreams are also common for non-spatial tasks, such as motor [44],
116 visuo-olfactive [45] and declarative [46] learning. Interestingly, dreams relate not only to
117 past waking life events but can also incorporate anticipated events (e.g., [60, 61]),
118 especially during late-night dreaming [41, 58], which may be analogous to imaginary or
119 prospective replays. Simulation of potential future scenarios has even been suggested as
120 the core biological function of dreaming [62, 63].

121 ***Selectivity***

122 The reactivation of memories in sleep appears to be a selective process. In rodents,
123 hippocampal memory traces of novel experiences, compared to familiar experiences, are
124 preferentially reactivated during sleep [14, 15] and persist longer [6, 8, 10]. Neural
125 reactivations in rodents are also amplified for experiences associated with an emotional
126 response [64] or a reward [65], potentially due to coupling of reactivations with dopamine
127 reward signals (e.g., [66, 67]) or with amygdala activity [64].

128 As observed for memory reactivations, dreams preferentially incorporate novel [68, 69],
129 emotionally intense (e.g., [70, 71]), and personally meaningful (e.g., [40, 72]) experiences.
130 However, one study found that enhancing the reward value of learned information did not
131 increase its incorporation into dreams [73].

132 In sum, while the reactivation of spatial memory has been most studied, newer research
133 suggests that other types of memory are also reactivated. This aligns better with dream
134 content, which contains spatial aspects, but is often centered on social, perceptual, and
135 emotional experiences. Beyond reactivating the past, both memory reactivations and
136 dreams can also be oriented toward the future, simulating anticipated trajectories or
137 scenes. Several factors, such as recency, emotional intensity, and novelty, modulate
138 which experiences are processed both for memory reactivation and dreams.

139 **When do neural reactivations and dreaming occur?**

140 ***Variations across sleep stages***

141 Neural reactivations in rodents have been consistently recorded in NREM sleep and
142 resting wake (Box 2). In fact, recordings of reactivations are often limited to short sleep-
143 onset periods following learning [19] (Box 3). In humans, direct evidence of memory
144 reactivations with intracranial recordings was found at sleep-onset [32], as well as in light
145 and deep sleep [30, 31, 33]. While memory reactivations appear to be closely related to
146 SWRs, which occur predominantly in these stages (e.g., [19]), they can also be found
147 outside of ripple events [6, 11, 74, 75]. Only few studies so far have reported neural
148 reactivations in REM sleep. One study has shown that neural replays, i.e., the reactivation
149 of information following a specific sequence, can occur in the hippocampus during REM
150 sleep [7], but their presence in REM sleep is still a matter of debate (e.g., [11, 76]).
151 Nonetheless, the application of other methods, e.g., decoders, has hinted at the possibility
152 that non-sequential reactivation of recently learned materials may occur in REM sleep in
153 rodents [77, 78] and humans (e.g., [29, 35, 79]).

154 In contrast with the reactivation literature, studies persistently show that dreams are more
155 salient and frequently recalled in REM sleep (over 80%) compared with NREM sleep
156 (~50%) [80]. However, it is also well established that vivid dream imageries can take place
157 during sleep onset (e.g., [81]) and that a wide range of oneiric activity occurs throughout
158 NREM sleep [80]. Beyond frequency of recall, the content of dreams also varies with
159 sleep stages. N2 and N3 dream reports are usually shorter, more thought-like, more
160 realistic, and contain more episodic material [80, 82, 83]. In contrast, REM dream reports
161 are longer, more 'story-like', more bizarre and emotional, and contain more semantic
162 knowledge [80, 84]. This suggests that the neurophysiology of REM sleep provides the
163 optimal conditions both to produce vivid dreams and for the cognitive processes
164 necessary for their recall.

165 ***Time course***

166 We know little about the time course of memory reactivations across one or multiple
167 nights. Most studies on memory reactivations have only analyzed short periods of sleep
168 immediately following a learning period, as tracing a specific neuron or even multiple

169 neurons over longer time is technically challenging. These studies show that the strength
170 of memory reactivation usually decays rapidly within the first hour spent asleep [8, 11, 51,
171 85]. However, a recent study reported that memory traces can be reactivated for up to 10
172 hours following a novel experience [10]. Ribeiro et al. [86] also reported longer-lasting
173 “reverberations” of neural activity patterns up to two days following a novel experience –
174 but it’s unclear if these prolonged effects were due to the analysis technique used in that
175 study [85]. Louie et al. [7] showed that, in rodents, REM sleep is more likely to replay
176 familiar spatial experiences, rather than novel experiences, in the sleep periods occurring
177 right before maze running. This time course differs from NREM sleep which tends to
178 replay recent awake behavior right after maze running. While evidence is limited, the time
179 course of neural reactivations may thus vary by sleep stages and time of night.

180 The recency of an experience also strongly affects its incorporation into dreams. Day
181 residue, i.e., incorporating events from the day before, is especially common in dreams
182 (e.g., [40, 41]), such that 50-70% of dreams relate to the previous day [87]. Studies show
183 that recent memories are more frequent in early-night sleep, especially in hypnagogic
184 imageries at sleep onset [88-90]. In contrast, late-night dreams incorporate more distant
185 memories [90, 91]. A dream-lag effect, whereby events that occurred 5-7 days earlier are
186 more likely to be incorporated into dreams [87], has been reported for REM but not NREM
187 dreams [92, 93]. Furthermore, memories from many days, months, and even years in the
188 past can still get incorporated into dreams [40, 41, 60, 90]. It was suggested that these
189 remote memories could be called upon in dreams through their association with recent
190 events, either to integrate novel experiences into pre-existing memory networks or to
191 maintain and update memory schemas (e.g., [94]).

192 In sum, memory reactivations are most consistent with the characteristics attributed to
193 NREM dreams, especially during the sleep onset period. However, the lack of studies on
194 remote memory reactivations in both NREM and REM sleep makes it hard to compare
195 them with the variety of memory sources present in dreams.

196 **How are memories reactivated?**

197 ***Speed and duration***

198 Several studies show that neuronal reactivations during sleep can occur at a faster time
199 scale than the original activity (e.g., [9, 12, 13, 20]), with compression factors as high as
200 5-10 times in the hippocampus (e.g., [12]). Neural reactivations in sleep are mostly
201 forward but can sometimes run backward [95]. Reactivations are short and can occur
202 within SWRs events in the order of 100 ms. However, they can also be combined into
203 longer sequences [96, 97] and thus last longer. In humans, learned motor patterns can
204 be replayed 1 to 4 times faster in the motor cortex during sleep [33]. Yet, other human
205 intracranial studies have shown no sign of temporal compression [30, 31]. There is also
206 evidence in rodents that neural reactivations can unfold at real-world speed in REM sleep
207 [7], NREM sleep [86] and waking rest [98]. It is still unknown why and in what contexts
208 neural reactivations occur in an accelerated fashion or in real time.

209 Whether similar temporal dynamics exist in dreams is unclear. In fact, the question of
210 temporality in dreams has long been the object of many debates (e.g., [99, 100]). One
211 study reported that dreams could be perceived to be much longer than the associated
212 REM sleep period [101]. However, this might be due to time perception biases that can
213 also occur during wake [102]. Several experimental studies have challenged the idea of
214 time compression or 'accelerated dreaming', showing that participants' estimation of
215 dream duration usually corresponds to the length of REM sleep preceding wakefulness
216 [103, 104]. More direct evidence comes from studies of lucid dreamers who can, using a
217 pre-established eye signal from within the dream state (e.g., move the eyes from left to
218 right three times), give a reliable and recordable time stamp of dream activity. These
219 studies have shown that counting in a **lucid dream** occurs at about the same speed as
220 in wake, and performing motor activities, such as walking, is even slower than in wake
221 [105, 106]. However, the timescales of conscious experiences may differ depending on
222 the level of lucidity and sleep stages. While REM and NREM dreams are usually
223 described as involving some sense of duration, hypnagogic imagery occurring at sleep-
224 onset – when most neural reactivations have been studied – can be experienced as
225 instantaneous, fleeting, and rapidly changing images [57].

226 ***Fidelity of replay***

227 A growing body of research shows that, beyond time compression, memory reactivations
228 do not often faithfully replay neural activity from an awake experience [74, 107]. Awake
229 reactivations tend to have greater fidelity to the original experience than sleep
230 reactivations [18, 108]. Some studies further show that NREM neural reactivations
231 occurring in early sleep cycles are more faithful to the original memory than those in later
232 cycles [77, 109]. It was hypothesized that higher-fidelity reactivations in wake might
233 support the initial stabilization of memories, while lower-fidelity reactivations in sleep may
234 play a broader role in the integration and generalization of memory across experiences
235 [108]. Mahoney et al. [96] showed that fragments of memory sequences are more often
236 reactivated than complete sequences and that these short bouts of memory can combine
237 to create longer sequences. One recent study has also shown that associated memories
238 can be co-reactivated in sleep, the disruption of which prevents the assimilation and
239 generalization of recent learning [110]. The fragmented and low-fidelity nature of neuronal
240 reactivations could explain the mixed results concerning the presence/absence of
241 memory reactivations in REM sleep: less faithful reactivations in this stage would be more
242 challenging to detect, and it becomes more debatable if they are actual reactivations (Box
243 3).

244 Similarly, dreams frequently incorporate memory elements but they rarely replay them in
245 their original entirety [58, 69, 94]. Indeed, a high similarity between dream content and
246 the actual episodic experience occurs in less than 2% of dreams [39, 111]. One exception
247 is the case of replicative nightmares that can, at times, replay traumatic memories as they
248 are remembered (e.g., [112]). Memories are more closely represented in NREM [113] or
249 early night [48, 91] dreams. In contrast, late-night dreams are more hyper-associative,
250 i.e., more bizarre, metaphorical, and related to distant memories [90, 91, 114]. Studies
251 looking at the incorporation of learning tasks in dreams in relation to performance also
252 show that the original memory task is not directly or fully incorporated in dreams, but that
253 dreams include the task in an indirect, associative, and fragmented way (e.g., [42, 47,
254 115]). Dreams tend to co-activate multiple memories within the same narrative [40, 41,
255 90, 114], possibly reflecting the integration and transformation of memory traces beyond
256 pure stabilization.

257 In sum, the existence of temporal compressions and the short duration of reactivations
258 can be difficult to reconcile with the temporal structure of dreams. While some level of
259 perceptual awareness is possible when complex stimuli are presented for only 50 – 100
260 ms when awake [116], such events are potentially too fast to create stable
261 representations in dreams, though they may still be able to influence their content. Yet,
262 memory reactivations and dreams are similar in that replay can happen in a transformed
263 and fragmented manner, especially later at night, and can co-activate multiple memories
264 at once.

265 **Neural correlates**

266 ***Anatomical correlates***

267 Memory reactivations were recorded both at the hippocampal level and in different cortical
268 and subcortical regions, including the prefrontal cortex [20, 117], motor cortex [16, 21],
269 visual cortex [6], entorhinal cortex [118], ventral tegmental area [67, 119], and ventral
270 striatum [76]. Cortical reactivations can be synchronized across distinct areas (e.g., [120])
271 and may be driven by hippocampal reactivations (e.g., [6, 64, 67, 76]).

272 The neural correlates of dreams are still a matter of debate (e.g., [121, 122]).
273 Nonetheless, cortical brain activity appears crucial to the emergence of conscious sleep
274 experiences [123, 124]. In fact, evidence collected through different techniques, including
275 high-density EEG [125, 126], fMRI [127, 128], and direct brain stimulation [129], suggests
276 that dream content may reflect the activation of the same brain areas typically involved in
277 similar experiences during wakefulness. The possible role of the hippocampus in the
278 generation of dream experiences is less clear but is partly supported by case studies on
279 patients with hippocampal damage (Box 4).

280 ***Functional correlates***

281 During NREM sleep, hippocampal SWRs associated with reactivation events are
282 coordinated with cortical **spindles** (10-16 Hz), which in turn tend to be phase-locked with
283 **slow oscillation** (<1 Hz) up-states [130]. In line with this, learning-related reactivations
284 time-locked to spindles [131-133] and slow-oscillation-spindle complexes [34] have been
285 shown in humans. Importantly, slow oscillations and spindles occur and are regulated

286 locally and are thus thought to sustain circuit-specific hippocampus-cortical coupling and
287 memory consolidation [134]. Although much less frequently than in NREM sleep, SWRs
288 may also be embedded into theta waves (4-12 Hz [19]) and sawtooth waves (2-6 Hz
289 [135]) during REM sleep. Moreover, transient increases in theta activity during phasic
290 REM periods are associated with increased coordination throughout the hippocampus
291 and cortical areas [136, 137]. In accordance with these observations, so-called **targeted**
292 **memory reactivation** (TMR; Box 1) [138] protocols, which induce memory reactivation,
293 may lead to increases in spindle (e.g., [139-141]), slow-wave (e.g., [142-144]), and/or
294 theta activity [144-146].

295 Sleep periods followed by a dream report, compared to those with no reported dream,
296 appear to be associated with a relative cortical activation and a decrease in **slow-wave**
297 **activity** during both NREM and REM sleep (review in [121]). In NREM sleep, dream recall
298 is associated with the occurrence of few and large slow waves on a relatively 'activated'
299 background and (fast) spindles [147, 148]. In REM sleep, an association between theta
300 activity and dream recall also received partial support [149, 150]. Moreover, some studies
301 reported positive associations between theta power and the incorporation of recent
302 memories into REM dreams [47, 151], but the reverse was found during the wake-sleep
303 transition [88].

304 Overall, the described findings indicate a partial overlap between the anatomical and
305 functional correlates of memory reactivation and those subserving the emergence of
306 oneiric experiences. However, direct evidence indicating that specific reactivation
307 patterns correspond with equally specific conscious experiences is yet to be obtained.

308 **Concluding Remarks and Future Perspectives**

309 In sum, some similarities between dreaming and memory reactivations during sleep
310 support the interpretation that neuronal reactivations are somewhat reflected through
311 dreams: both include fragments of recent experiences, have a bias for salient and novel
312 memories, show lower-fidelity reactivations later in the sleep period, share some of the
313 underlying neural correlates and are associated with improved performance. Studies
314 manipulating memory reactivations, although limited in scope, have shown evidence for

315 both direct and delayed influence on dreams (Box 1). However, several characteristics of
316 memory reactivations have no clear phenomenological equivalent in dreams. Most
317 memory reactivations are present in quiet wake, drowsiness, or early NREM sleep, are
318 related to slow-oscillation activity and tend to decay across a sleep period. In contrast,
319 dreaming is most prominent (and 'dream-like') when slow-oscillation activity is lower,
320 especially in late REM sleep. Further, most evidence points towards dreams playing at
321 real-life speeds and taking place across seconds and minutes, while reactivations are
322 often compressed and can take place in the range of hundreds of milliseconds. Lastly,
323 hippocampal damage does not prevent dreaming from occurring, although it may affect
324 its frequency and content across sleep stages. Overall, these findings cast doubt on the
325 interpretation that dreams directly reflect memory reactivations. Instead, it seems
326 plausible that only neural reactivations occurring in trains and at non-compressed speeds
327 are consciously experienced during sleep. The conscious and interactive experience of
328 dreaming likely goes beyond the mere reflection of memory reactivations, potentially
329 supporting broader functions of memory integration, sense-making, emotional regulation,
330 and preparation for the future (e.g., [94, 152]). In this view, neural reactivations may still
331 partly make their way into dream content, contributing to the memory elements that are
332 processed and integrated into rich and multisensory dream experiences. Alternatively,
333 memory reactivations may not be immediately or directly perceived in dreams but rather
334 play a role in selecting or priming memory traces that are, only at a later stage, processed
335 at the cognitive level in dreams. Our current knowledge of the two phenomena does not
336 conclusively support a sole interpretation. Future research will have to overcome several
337 limitations to advance our understanding of how they are related.

338 Memory consolidation is a process that unfolds over time – however, due to
339 methodological restrictions, our understanding of the time course of memory reactivations
340 within a single night and especially across multiple nights is still lacking. Recently
341 proposed frameworks suggest that within a single night, the combination of high-fidelity
342 replay of recent memories in early NREM sleep with lower-fidelity replay, and integration
343 with more remote memories, in later REM sleep optimizes memory consolidation over
344 time (e.g., [153, 154]). However, experimental data from rodent and human research to
345 verify these models are still lacking. This will potentially require the development of new

346 methods to trace remote and lower fidelity memory reactivations, as well as methods to
 347 detect co-reativations of multiple memory sources over longer periods. Further, more
 348 research on non-spatial memory reactivation (e.g., emotional or cognitive content), which
 349 makes up the majority of dream content, will shed light on potential similarities between
 350 the two. On the dream research side, some limits need to be overcome. Currently, many
 351 studies in human dream research have small sample sizes, low sampling of dreams, rely
 352 on the ability of participants to recollect their dreams or memories in detail, and are often
 353 correlational. Using new approaches to manipulate memory processes during sleep, such
 354 as TMR, and approaches to manipulate dreaming, such as induced lucid dreams, will
 355 allow a more mechanistic understanding of how memory reactivations are linked to
 356 dreaming. Collecting dream reports in patients with intracranial recordings would also
 357 present an exciting opportunity for directly comparing dreaming and memory reactivation.
 358 Further developing sleep and dream engineering methods [155], together with
 359 neurophenomenological approaches aimed at rigorously collecting and analyzing dream
 360 content, may help unveil the complex relationships between dreaming and memory.

361

362 Table 1. Summary of comparison points between memory reactivation and dreaming

	Memory reactivation	Dreaming
What		
Content	<ul style="list-style-type: none"> • Most evidence for spatial memory • Evidence for motor, visual and social memories • Prospective replay/pre-play 	<ul style="list-style-type: none"> • Spatial content is present but often vague/discontinuous • A variety of experiences (motor, visual, social, sensory, cognitive, emotional, etc.) • Anticipated events
Selectivity	<ul style="list-style-type: none"> • Novel • Emotional • Potentially rewarding 	<ul style="list-style-type: none"> • Novel • Emotional/Salient/Meaningful • No evidence for rewarding events
When		

Sleep stages	<ul style="list-style-type: none"> • Most prevalent in quiet wake and NREM sleep • Limited evidence in REM sleep 	<ul style="list-style-type: none"> • Occurs in all sleep stages • Most vividly recalled from REM sleep • NREM dreams are more episodic • REM dreams contain more memory sources and are more hyper-associative
Time course	<ul style="list-style-type: none"> • Early sleep • Decay with time • Limited evidence for late sleep • Methodological difficulties for measuring across days 	<ul style="list-style-type: none"> • Throughout the night • More vivid at the end of the night • Recent memory sources at the beginning of the night • More remote memory source at the end of the night • Temporal trends (day residue and dream-lag effect)
How		
Speed & Duration	<ul style="list-style-type: none"> • Compressed (up to 10x speed) or normal speed • Duration in the order of 100 ms • Single reactivations can be combined into longer sequences 	<ul style="list-style-type: none"> • Relatively normal speed (lucid dreams) • Time distortion can be present • Estimated length varies from seconds to minutes
Fidelity of replay	<ul style="list-style-type: none"> • Fragments of experience • Transformed (lower fidelity in sleep than awake) • Lower fidelity in later sleep • Can combine multiple memories 	<ul style="list-style-type: none"> • Fragments of experiences • Transformed (rarely episodic replay) • Lower fidelity (more hyperassociative) in later sleep • Can combine multiple memories
Neural correlates		

Anatomical	<ul style="list-style-type: none"> • Hippocampus and cortical regions • Hippocampal reactivations might drive cortical reactivations 	<ul style="list-style-type: none"> • Cortical Regions • Hippocampal contribution to frequency and richness of content
Functional	<ul style="list-style-type: none"> • Sharp wave-ripples • Slow oscillations and spindles • Theta waves 	<ul style="list-style-type: none"> • More scarce evidence • Dream recall associated with spindles, theta activity, and lower slow-wave activity • Memory incorporations related to theta activity

363 **Glossary**

364 **Active system consolidation:** A model of memory consolidation during sleep whereby
365 newly formed memory traces in the hippocampus are reactivated during sleep, which
366 drives their gradual redistribution into longer-term neocortical storage.

367 **Lucid dream:** A dream when the dreamer becomes aware that they are dreaming while
368 remaining asleep.

369 **Memory reactivation:** Patterns present during learning/encoding that are activated again
370 more strongly after than prior to learning/encoding. The pattern does not have to be
371 measured on the individual neuron level but can be present in any measuring technique
372 or analysis method [156].

373 **Neural replay:** A specific form of reactivation that includes sequential (temporal and/or
374 spatial) information. The sequence does not have to be a perfect replicate of the original
375 but can contain, e.g., fewer spikes when measured in unit activity or different temporal
376 dynamics as speed-up or stationary moments [156].

377 **Non rapid eye movement (NREM) sleep:** A sleep stage characterized by low frequency
378 EEG signals with distinct patterns (slow waves, spindles, K-complexes), which can be

379 further divided into three substages (N1, N2, N3). It occurs in cycles with REM sleep
380 throughout the night and is associated with less, and more thought-like, dreams.

381 **Pre-play:** Temporal patterns of activity that are correlated with the patterns that will arise
382 during a future novel experience, thought to be the neuronal structure new memories are
383 mapped onto [156].

384 **Rapid eye movement (REM) sleep:** A sleep stage characterized by rapid eye
385 movements, low amplitude mixed frequency EEG and low muscle tone that occurs in
386 cycles with NREM sleep throughout the night and is associated with frequent, vivid, and
387 story-like dreams.

388 **Sharp wave-ripples (SWRs):** Bursts (50 – 150ms) of Ca1 hippocampal pyramidal
389 neurons activity (~30% of neurons) within distinct high-frequency (100-250 Hz, ripple)
390 fluctuations in the hippocampal local field potential after input of Ca3 (sharp wave).

391 **Slow oscillations:** Cycles of cellular activity <1 Hz as a periodic process (Hz),
392 consisting of an alternation of active (upstate) and silent (downstate) states [157].

393 **Slow wave activity:** Wave activity in scalp EEG or intracranial EEG, in the delta
394 frequency 0.5–4.5 Hz, or subsets within this frequency [157].

395 **Spindles:** Burst of neural oscillatory activity in the range of 10 – 16 Hz with a duration of
396 longer than 0.5 seconds present during NREM sleep.

397 **Targeted Memory Reactivation (TMR):** A method to manipulate memory during sleep
398 by playing a stimulus associated with a memory during sleep below awakening threshold.

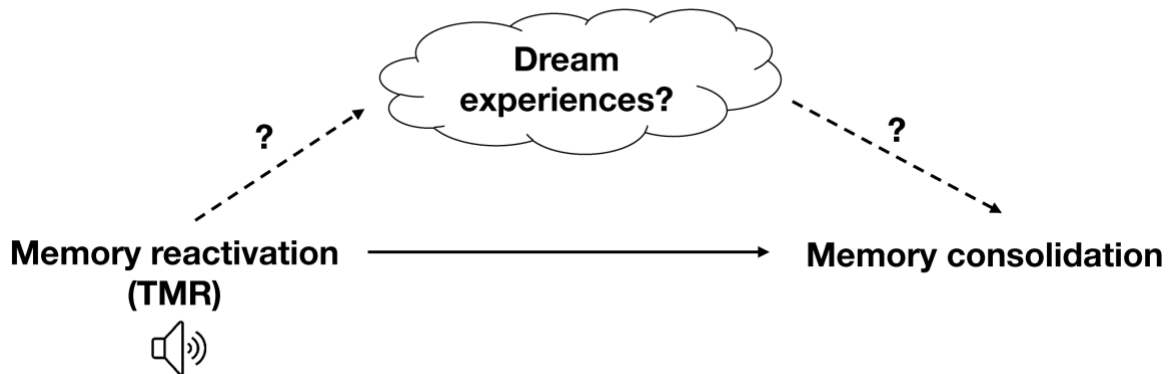
399 **Text boxes**

400 **Box 1. Targeted memory reactivation and dreaming**

401 Research from the last 15 years suggests that memory reactivations during sleep can be
402 experimentally biased in humans. Targeted memory reactivation (TMR) is a procedure
403 which consists of pairing a stimulus, such as a sound or a smell, with task learning and
404 then re-exposing participants to this stimulus during sleep to reactivate this specific
405 learning [158]. In rodents, it was shown that TMR biases the content of memory

406 reactivations that occur in the following 1-2 s towards the associated task [109], while
407 several human studies have shown that TMR has a beneficial effect on memory
408 performance (see meta-analysis [159]).

409 The effect of TMR on mental experiences during sleep has only been explored in a few
410 studies. In pioneering work, Hervey de Saint-Denys [160] experimented with sounds,
411 smells, and tastes to associatively modulate the content of his dreams. For example, he
412 associated distinct perfume smells to different locations – several months later, a drop of
413 a perfume associated with the Vivarais countryside on his pillow triggered a dream of
414 mountains and chestnut trees reminiscent of this place. Similarly, in laboratory studies,
415 the presentation during sleep of a rose smell, previously associated with rural images,
416 increased references to the countryside in dreams, however, this did not work for a smell
417 associated with urban images [161]. De Koninck and Koulack [162] were also able to
418 increase dream incorporation of a stressful movie viewed before sleep after replaying the
419 movie soundtrack at low levels during REM sleep. A pilot study combining the ticking
420 sound of a clock with a mirror tracing task showed that the clock sound, when replayed
421 during phasic REM sleep, was associated with changes in dream content reminiscent of
422 the task [163]. Using a similar approach with a flying simulation in virtual reality, Picard-
423 Deland et al. [164] showed that TMR had only a delayed effect on dreams, such that TMR
424 applied in REM sleep led to more dreams of the task in the following two days, while TMR
425 applied in NREM sleep led to more dreams about the task 5-6 days later. Moreover, this
426 was the first study to link TMR and dreaming to memory performance, showing that TMR
427 in REM sleep had a beneficial effect on motor learning only in participants who
428 concurrently dreamed about the task [47]. More well-designed laboratory studies are
429 needed to investigate the influence of TMR on dreams and whether dream incorporations
430 are relevant to memory performance (Figure I).



431

432 **Figure 1. Targeted memory reactivation protocols can be used to clarify the**
 433 **relationships between memory reactivation, subjective dream experiences and**
 434 **memory consolidation.**

435

436 **Box 2. From mind-wandering to dreaming – a continuum of reactivation**
 437 **processes?**

438 Neural reactivations as a mechanism for memory consolidation have been initially
 439 associated with sleep only. However, in recent years both animal and human research
 440 have been increasingly studying memory reactivations also during wakeful resting states.
 441 Considerable evidence suggests that even brief bouts of offline rest periods during
 442 wakefulness can benefit memory consolidation [165].

443 Prima facie this might be seen as a strong counterargument to the idea that dreaming
 444 represents the subjective experience of memory reactivations. However, just as with
 445 reactivations, the study of intrinsically originating mental processes is not restricted to
 446 sleep and is increasingly expanded to wakefulness: spontaneous thoughts and imagery
 447 are considered a continuum across the sleep-wake cycle, experienced as dreaming
 448 during sleep, and as mind-wandering during wakefulness [166]. Outside of academic
 449 research, this idea is already emphasized by the folk psychology notion of daydreaming.

450 Despite some described differences, such as mind-wandering being more future-oriented
 451 (including autobiographical planning), including more episodic thoughts, and being more
 452 positively valenced than dreaming [167, 168], many obvious similarities exist: both mind-

453 wandering and dreaming happen involuntarily, are largely independent of external stimuli,
454 follow loose narratives related to current concerns, and are characterized by a relative
455 lack of meta-awareness [166]. Also, periods of apparently ‘empty’ conscious experiences
456 have been described for both mind-wandering and dreaming, dubbed as ‘mind blanking’
457 and ‘white dreams’, respectively [169].

458 On the brain level, considerable similarities can also be identified: both mind-wandering
459 and REM sleep are associated with activation in cortical regions of the default mode
460 network [166]. In addition, episodes of mind-wandering during wakefulness have been
461 associated with temporally and/or spatially localized intrusions of sleep-like oscillatory
462 activity [169]. Notably, SWRs, as a crucial neural mechanism of memory reactivations,
463 can be recorded during both sleep and rest. On the subjective level, SWRs have been
464 suggested as a physiological substrate for priming spontaneous mental activity during
465 periods of rest [19]. However, just as in the case of dreaming, the timing of SWRs and
466 reactivations are at odds with the phenomenal timing of mind-wandering.

467 In summary, memory reactivations during wakefulness do not fundamentally speak
468 against the idea that dreaming represents the subjective experience of neural
469 reactivations, as multiple phenomenal and neural similarities exist between dreaming and
470 mind-wandering. Therefore, arguments for and against memory reactivations as a
471 substrate of (day-)dreaming appear to be applicable to either state.

472

473 **Box 3. Investigating memory reactivation in rodents – methodological** 474 **implications**

475 When comparing dreaming to memory reactivations, it is essential to be aware of the
476 methodological challenges of rodent research. The biggest challenge is creating an
477 experimental setup that obtains sufficient statistical power for analysis, which has led to
478 studies including 1) roughly 20 mins of active behavior (to reliably detect neuronal
479 patterns), 2) low behavioral variability, 3) easily repeatable tasks (to ensure maximum
480 data per animal), and 4) short recording durations (to allow for multiple experiments per
481 day). This often leads to studies overtraining animals on simple tasks (e.g., track running),

482 and to limited recording time (1-2 h) after training. Depending on time of day and
483 habituation, an animal will sleep 30-60% of those initial hours after training [26] - mainly
484 remaining in NREM sleep, which often prevents analyzing potential REM reactivations.
485 Most of the time, the animal will be quietly resting, which might better correspond to
486 wakeful rest or N1 sleep in humans rather than N2 or N3 sleep [170]. As most reactivation
487 studies in rodents do not perform sleep scoring, it is often unclear which state the memory
488 reactivations are recorded from; even when sleep scoring is done, studies rarely
489 distinguish between different NREM sleep stages, but may instead consider all NREM
490 stages as “slow-wave sleep” (SWS) [5]. Therefore, caution is necessary when comparing
491 human and rodent studies.

492 A further complication is that different studies use different methods to measure memory
493 reactivations [171] and no systematical evaluation has been done on how methodological
494 differences influence the obtained results. For example, as NREM reactivations are less
495 faithful to the original experience than wake reactivations [108], reactivation analyses that
496 depend on a high match of the neuronal pattern will pick up fewer reactivations in sleep
497 than other methods. This might explain contradictory findings on REM reactivations.
498 Newer techniques, such as calcium imaging, promise to help overcome some of these
499 issues, e.g., by allowing tracking neurons for longer periods. However, calcium dynamics
500 differ between sleep and wake [172], and individual spikes – which are common during
501 reactivations – do not lead to calcium influx.

502 In sum, current methodological issues in rodent studies are hampering more detailed and
503 longer-term investigations of memory reactivations. The reactivations of remote events
504 are especially difficult to show with these techniques. Developing techniques and study
505 designs to detect the reactivation of remote events would be of great value to further our
506 understanding of how dreaming and memory reactivations are linked.

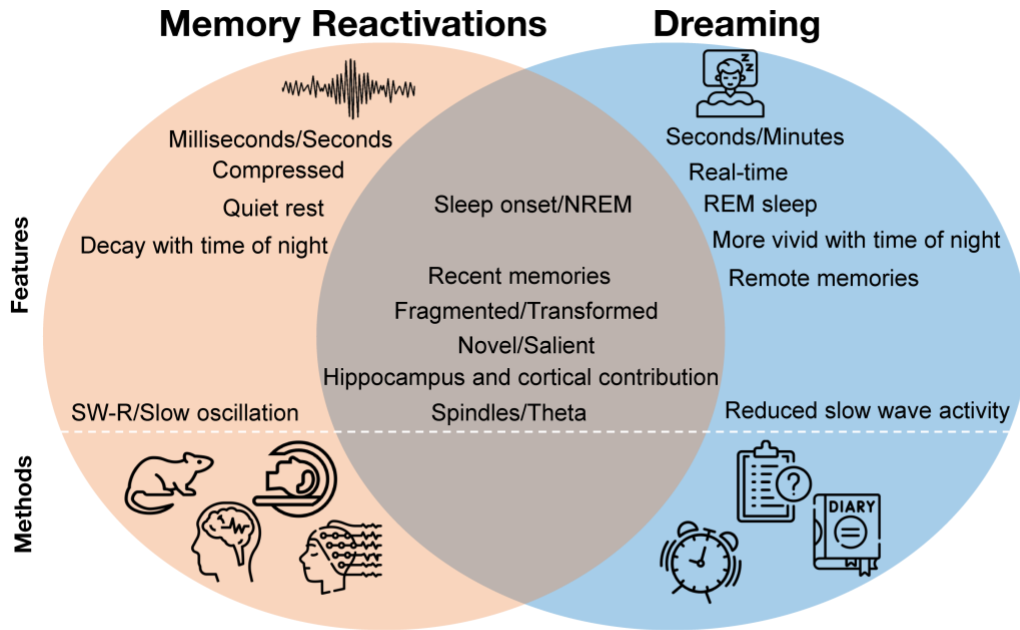
507

508 **Box 4. Insights from case studies with hippocampal damage**

509 Memory reactivations are closely tied to hippocampal SWRs, but the role of the
510 hippocampus in the generation of dreams remains unclear. Theories have suggested that

511 changes in hippocampal activity occurring during REM sleep contribute to some of the
512 unique characteristics of dream content (review in [173]). Still, this view has yet to be
513 supported by empirical evidence. The study of dreams in patients with hippocampal
514 damage, with altered memory for episodic events, may nonetheless shed light on how
515 they are related. A recent study compared four patients with hippocampal damage to a
516 control group. They collected dream reports after awakenings from REM and NREM sleep
517 and reported fewer dreams in patients than in the control group from either sleep stage.
518 The patient's dream content included fewer episodic details and lacked content [174].
519 This aligns with an early study from Torda [175, 176], which compared REM dreams from
520 awakenings from 3 patients with bilateral hippocampal lesions and amnesia to healthy
521 controls and found that the patients reported fewer dreams and that their dreams were
522 shorter, simpler, reality-bound, and lacked daily residue as well as emotional depth.
523 Temporal lobe epilepsy has also been associated with repetitive bad dreams with
524 stereotypical content [177]. Solms [124], however, did not find an effect of hippocampal
525 damage on dreaming. As a specific type of dreaming, hypnagogic imagery has been
526 shown not to be affected by hippocampal lesions. Amnesic patients still reported the
527 stereotypical visual imagery at sleep onset after playing Tetris, despite not remembering
528 that they played the game [89]. Interestingly, hippocampal damage also affects
529 daydreaming, patients engaged in similar levels of mind-wandering compared to control
530 participants, but with mainly abstract and verbal content with limited capacity to imagine
531 past or future episodes [178]. Beyond hippocampal damage, one study shows that
532 hippocampal microstructure is associated with dreaming. While the number of dreams
533 did not relate to the amygdala or hippocampal volume and microstructure, there were
534 slight associations between dream bizarreness and hippocampal microstructure [179].
535 Overall, the involvement of the hippocampus in dream formation has been contested by
536 some early studies on patients with hippocampal damage but found support in more
537 recent investigations. These findings suggest that dream activity may persist in case of
538 hippocampal damage but that the hippocampus influences its frequency, richness, and
539 content.

540 **Figures**



541
 542 **Figure 1. Overview of the dreaming and memory reactivation comparison.** While
 543 both phenomena share some features (shaded area), there are also some differences
 544 between dreaming (blue) and memory reactivations (orange). Furthermore, very different
 545 methods are used to research dreaming and memory reactivations. While memory
 546 reactivation research is mostly done in rodents, several studies also research it in humans
 547 using intracranial EEG, high-density EEG and fMRI. Dream research, on the other hand,
 548 relies on subjective reporting by participants using questionnaires, diaries and serial
 549 awakenings. SW-R = sharp wave-ripples, REM = rapid eye movement, NREM = non rapid
 550 eye movement. Icons from flaticon.

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