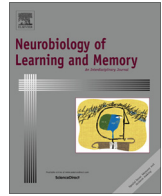




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Review

The role of rapid eye movement sleep for amygdala-related memory processing

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ABSTRACT

Over the years, rapid eye movement (REM) sleep has been associated with general memory consolidation, specific consolidation of perceptual, procedural, emotional and fear memories, brain maturation and preparation of waking consciousness. More recently, some of these associations (e.g., general and procedural memory consolidation) have been shown to be unlikely, while others (e.g., brain maturation and consciousness) remain inconclusive. In this review, we argue that both behavioral and neurophysiological evidence supports a role of REM sleep for amygdala-related memory processing: the amygdala–hippocampus–medial prefrontal cortex network involved in emotional processing, fear memory and valence consolidation shows strongest activity during REM sleep, in contrast to the hippocampus–medial prefrontal cortex only network which is more active during non-REM sleep. However, more research is needed to fully understand the mechanisms.

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1. Introduction

Since the first empirical reports on the positive effects of post-learning sleep on memory consolidation (Jenkins & Dellenbach, 1924), a large body of evidence has confirmed the sleep–memory relationship (Diekelmann & Born, 2010). Sleep consists of a cyclic alternation between non-REM sleep (NREM), which can be subdivided into the stages 1 through 4 with stages 1 and 2 known as light sleep and 3 and 4 as slow wave sleep, and REM sleep. While evidence for the neural mechanisms occurring during non-REM (NREM) sleep – memory replay and downscaling – has been accumulating, the role of REM sleep still remains elusive. During NREM sleep, slow oscillations are thought to entrain hippocampal sharp wave ripples to enable replay in the hippocampus and prefrontal

cortex, which is then followed by sleep spindles for local, cortical processing (Genzel, Kroes, Dresler, & Battaglia, 2014). Sleep spindles may also occur independently, most likely to facilitate the consolidation of cortical networks independent of hippocampal led replay. This mechanism of active reprocessing of memories is then followed by a more general downscaling mechanism during the delta waves of deep sleep to enhance the signal to noise ratio (Genzel et al., 2014; Tononi & Cirelli, 2014). Together the “push” of relevant memory traces during replay and “pull” of downscaling is thought to enable extraction of statistical overlap across different episodic memories leading to semanticized memories in the cortex (Battaglia, Borensztajn, & Bod, 2012; Genzel et al., 2014). These consolidation processes in NREM are succeeded by REM sleep in the NREM/REM cycle, but it remains unknown for what purpose.

Initially, REM sleep was associated with brain maturation and general memory consolidation, potentially associated with dream mentation. Further, for several years the most dominant theory was that REM sleep supports the consolidation of procedural

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84 memories like motor skills while NREM sleep supports declarative
85 memories like verbal information (Marshall & Born, 2007). How-
86 ever, more recent studies failed to confirm this mapping between
87 sleep stages and memory systems (Dresler et al., 2011; Genzel,
88 Dresler, Wehrle, Groezinger, & Steiger, 2009; Genzel et al., 2012;
89 Rasch, Pommer, Diekelmann, & Born, 2009; Dresler et al.). In this
90 paper, we will review the role of REM sleep for different memory
91 systems and other functions in humans and non-human animals
92 and provide existing evidence for and against each theory. Further,
93 we will go on to show that the most conclusive and consistent evi-
94 dence points toward a function of REM sleep in reprocessing of
95 information in amygdala–hippocampal–medial prefrontal cortical
96 networks, which may be enabled or mediated by the dominant
97 oscillations (PGO-waves and theta) as well as elevated levels of
98 acetylcholine and cortisol present in REM sleep. More specifically
99 it seems that REM sleep may serve the purpose of emotional
100 valence re-evaluation and adjustment, e.g., evaluating whether a
101 stimulus is associated with a specific outcome and either up or
102 Q6 down regulating the associated emotion encoded in the amygdala
103 (see Table 1).

104 2. REM sleep dreaming and memory consolidation

105 One of the most striking features of REM sleep is its subjective
106 phenomenology, i.e., dreaming. Dream-like mental activity can be
107 observed during all sleep stages, however REM sleep dreams are
108 particularly vivid and intense (Nielsen, 2000). Events and memo-
109 ries from waking life are sometimes incorporated into dreams,
110 either as classical day-residues in the following night or after a
111 “dream lag” of about 5–7 days (Blagrove, Henley-Einion, Barnett,
112 Edwards, & Seage, 2011; Nielsen, Kuiken, Alain, Stenstrom, &
113 Powell, 2004; Nielsen & Powell, 1989). Such dream incorporations
114 have been suggested to reflect processes of memory consolidation,
115 and indeed some studies support this view by showing that items
116 that were incorporated into dreams showed better memory reten-
117 tion (Cipolli, Fagioli, Mazzetti, & Tuozzi, 2004; de Koninck, Christ,
118 Hébert, & Rinfret, 1990).

119 On the neurophysiological level, dream mentation has been
120 suggested to represent the phenomenological reflection of a neural

replay of activation patterns associated with recent learning experi- 121
ences (Wamsley, 2014; Wamsley & Stickgold, 2011; Wilson & 122
McNaughton, 1994). Although one study demonstrated such reac- 123
tivations in REM sleep (Louie & Wilson, 2001), the most advanced 124
models of sleep-related memory consolidation propose that neural 125
replay is orchestrated by an interaction of hippocampal sharp wave 126
ripples, thalamo-cortical sleep spindles, and cortical slow oscilla- 127
tions during NREM sleep (Genzel et al., 2014; Molle & Born, 128
2011). In line with this view, more recent studies found a positive 129
effect of dream-incorporations of recent learning experiences on 130
later memory performance to be associated mainly with NREM 131
sleep (Wamsley, Perry, 2010; Wamsley, Tucker, 2010). Moreover, 132
despite a majority of dream reports having been judged to reflect 133
certain aspects of recent waking life experiences, an actual episodic 134
replay of waking events was found in no more than 1–2% of the 135
dream reports (Fosse, Fosse, Hobson, & Stickgold, 2003), with 136
NREM sleep dreams appearing to include more identifiable epi- 137
sodic memory sources than REM sleep dreams (Baylor & 138
Cavallero, 2001). However, it was suggested that particularly 139
engaging learning experiences have a more robust influence on 140
dream content, relative to more passive experiences which might 141
lead to underestimations of experience-related dream incorpora- 142
tions (Wamsley, 2014). Nevertheless, the REM sleep dream narra- 143
tive does not seem to reflect a simple replay of full episodic 144
memories for the sake of consolidation. 145

146 3. The role of REM sleep in memory integration and 147 reorganization

148 Besides a mere strengthening of recently acquired memories, 149
REM sleep has also been suggested to be involved in the integra- 150
tion of new information into existing knowledge structures, the 151
reorganization of these structures, and the generalization of 152
recently acquired memories. For example, auditory cues were 153
associated during encoding with pictures of faces and were later 154
delivered during REM sleep. The subjects later not only remem- 155
bered previously presented faces better, but also related face pic- 156
tures that have not been presented before (Sterpenich et al., 157
2014). This was not the case when the cues were delivered during

121 **Table 1**
122 Methodological approaches to REM sleep in humans.

Design	Design	Control	Caveats	Examples
Half-night paradigm	Contrasts the two night halves using the dominance of SWS during the first half of the night and REM sleep during the second half (encoding before and retrieval after the respective night half)	The other half of the night	Difference in encoding/retrieval conditions (early evening/middle of the night/early morning), hormone levels (growth hormone, cortisol)	Plihal and Born (1997)
Selective sleep deprivation – manual	Subject's sleep is scored online and they are awoken as soon as the respective sleep stage is reached	Control waking condition (other sleep stage e.g., SWS or random), undisturbed night	Can be stressful	Genzel et al. (2009)
Selective sleep deprivation – pharmacological	Certain antidepressants (e.g., SNRI) show REM sleep suppressed effects	Other antidepressants (e.g., SSRI)	Confounding effects of medication	Rasch et al. (2009)
Nap	Short daytime naps (60 min) usually contain little or no REM sleep, while longer naps (90 min) do	Wake control during the same time period	Day time naps may not be the same as night sleep in regard to hormones e.g., cortisol. Further usually only very little REM sleep is achieved (<15 min)	Genzel et al. (2012)
Effects of learning on sleep	Sleep with and without previous learning is compared	Sometimes similar encoding experience but without memory component	Unspecific effects of the encoding experience often not controlled for	Fogel et al. (2011)
Correlational analysis	REM sleep amount, REM density or REM spectral power are correlated with learning measures	None	Correlational, often not controlled for multiple comparison (e.g., the different sleep stages) and correlation for state (memory consolidation) can be confounded by trait	Peters, Smith, and Smith (2007)

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