Brain & Language 167 (2017) 94–105

Contents lists available at ScienceDirect

Brain & Language

journal homepage: www.elsevier.com/locate/b&l

Review

The beneficial role of memory reactivation for language learning during sleep: A review

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ARTICLE INFO

Article history:
Received 31 August 2015
Revised 19 January 2016
Accepted 18 February 2016
Available online 29 March 2016

Keywords:
Sleep
Language learning
Memory
Reactivation

ABSTRACT

Sleep is essential for diverse aspects of language learning. According to a prominent concept these beneficial effects of sleep rely on spontaneous reactivation processes. A series of recent studies demonstrated that inducing such reactivation processes by re-exposure to memory cues during sleep enhances foreign vocabulary learning. Building upon these findings, the present article reviews recent models and empirical findings concerning the beneficial effects of sleep on language learning. Consequently, the memory function of sleep, its neural underpinnings and the role of the sleeping brain in language learning will be summarized. Finally, we will propose a working model concerning the oscillatory requirements for successful reactivation processes and future research questions to advance our understanding of the role of sleep on language learning and memory processes in general.

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1. Introduction

In today's multilingual world, interaction amongst people with diverse cultural background and mother tongues is a permanent feature. Thus, learning and mastering new languages becomes increasingly important, and potential approaches to facilitate and accelerate tedious language learning processes are highly desirable for many of us. According to recent findings, sleep might be an ideal state for the application of such learning enhancing approaches (Diekelmann, 2014). Sleep after learning generally promotes divers aspects of language learning, ranging from word learning to the abstraction of grammatical rules (Batterink, Oudiette, Reber, & Paller, 2014; Henderson, Weighall, Brown, & Gaskell, 2012). Furthermore, emerging techniques as targeted

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http://dx.doi.org/10.1016/j.bandl.2016.02.005
0093-934X/

reactivation of language-related memory representations might fundamentally change how we learn foreign languages in the future.

In this review, we aim at presenting recent models and empirical findings concerning the beneficial effects of sleep on language learning, focussing particularly on studies that actively enhance specific aspects of language learning during sleep. Accordingly, the memory function of sleep and its role in language learning will be reviewed. Furthermore, we will summarize the ability of the sleeping brain to process auditory sensory input, constituting a fundamental requirement for divers learning enhancing techniques. On this basis we will present a series of recent findings concerning the targeted reactivation of foreign vocabulary by auditory cues during sleep, its impact on vocabulary learning and associated neural activity. Finally, we propose a working model on how oscillatory activity during sleep supports the reactivation, stabilization and integration of newly learned words. We conclude that enhancing language learning during sleep by targeted memory reactivation (TMR) provides an exciting new investigation tool, stimulating future research to further understand the neural mechanisms underlying sleep-benefits in language acquisition and consolidation.

2. Memory and sleep

Language learning is closely tied to basic processes of memory, which can be broadly divided into three core stages: encoding, consolidation and retrieval (Gabrieli, 1998). During encoding, new and initially labile memory traces are formed that are still highly susceptible to interference. During subsequent memory consolidation, these newly encoded memories are stabilized and strengthened. In addition, the new memory representations are gradually integrated into pre-existing knowledge networks on the cortical level for long-term storage. Finally during retrieval, memories are accessed and recalled.

While encoding and retrieval are clearly tied to the state of wakefulness, sleep plays a crucial role in the consolidation of newly encoded memories (see Rasch & Born, 2013, for a comprehensive review): Sleep after learning benefits memory consolidation, leading to stronger and better integrated memory traces after sleep, supporting improved retrieval performance. These beneficial effects of sleep on memory have been consistently demonstrated for diverse types of memories (Walker & Stickgold, 2004), ranging from priming, conditioning and procedural motor memories (Menz et al., 2013; Plihal & Born, 1995, 1999) to declarative episodic memories including vocabulary learning (Gais & Born, 2004; Gais, Lucas, & Born, 2006). Furthermore, sleep has been demonstrated to support processes of abstraction, inference, and insight (Ellenbogen, Hu, Payne, Titone, & Walker, 2007; Lewis & Durrant, 2011; Wagner, Gais, Haider, Verleger, & Born, 2004). First concepts were formulated almost a century ago and assumed that sleep might solely protect memories passively by a reduction of external interference after learning (Jenkins & Dallenbach, 1924). Since then, substantial evidence has accumulated indicating that the memory function of sleep goes far beyond these early assumptions by providing consistent support for an active role of sleep for the consolidation of memories (e.g. Born & Wilhelm, 2012; Gais et al., 2006; Walker & Stickgold, 2004). According to the theoretical account of active system consolidation during sleep (Diekelmann & Born, 2010), which we will describe in more detail below, a central aspect of the active role of sleep on memory consolidation is the notion that newly encoded memories are spontaneously and repeatedly reactivated during sleep. These reactivations are thought to stabilize and strengthen newly encoded memories for the long-term and to integrate them into pre-existing knowledge networks. Similarly, according to the recent version of the synaptic homeostasis hypothesis "synapses activated strongly and consistently during sleep survive mostly unchanged and may actually consolidate" (Tononi & Cirelli, 2014, page 15).

3. Memories are spontaneously reactivated during sleep

Supporting the notion of a critical role of reactivations during sleep for memory consolidation, replay activity during sleep has been consistently reported in memory-related brain structures, particularly in the hippocampus, in rodents as well as in humans (O'Neill, Pleydell-Bouverie, Dupret, & Csicsvari, 2010; Pavlides & Winson, 1989; Peigneux et al., 2004; Peyrache, Khamassi, Benchenane, Wiener, & Battaglia, 2009). Pioneering rodent studies could demonstrate that the spatial and even the temporal pattern of neuronal firing, occurring during exploration of a novel environment, are spontaneously reactivated in the same order during subsequent Non-rapid eye movement (NREM) sleep (Skaggs & McNaughton, 1996; Wilson & McNaughton, 1994). Succeeding experiments additionally indicated that spontaneous memory reactivations are typically time-compressed by a factor of 10–20 (O'Neill et al., 2010) and are closely related to specific oscillations in the hippocampus, the so called hippocampal sharp-wave ripples (SW-R, large amplitude sharp wave followed by a high frequency oscillation in the 200 Hz range) (Ylinen et al., 1995). Replay activity during sleep has not only been found in the hippocampus but as well in various other memory related brain regions (i.e., prefrontal cortex, ventral striatum, etc. (Ji & Wilson, 2007; Pennartz et al., 2004; Peyrache et al., 2009)), possibly mirroring the gradual redistribution and integration of memory representations in cortical brain structures.

Based on these findings, the active system consolidation theory postulates that the covert and repeated reactivations of newly encoded memories during NREM sleep sub-serve these system consolidation processes of reorganization and integration (Diekelmann & Born, 2010; Stickgold & Walker, 2013). System consolidation refers to the two-stage model of memory consolidation (Marr, 1971; McClelland, McNaughton, & O'Reilly, 1995), stating that initial encoding of memories critically relies on a fast learning memory system (i.e., the hippocampus for declarative memories). After encoding, the information is gradually redistributed into a second, slow-learning memory system in cortical brain areas and integrated into pre-existing knowledge networks. Thereby, memory representations gradually loose their retrieval-dependency on hippocampal structures. According to the active system consolidation theory, this process of gradual system consolidation is actively supported by sleep based on repeated memory reactivations interleaved with reactivation of associated older memories (Rasch & Born, 2007).

It is further assumed that the reactivation and redistribution of memory representation during post-learning sleep is closely linked to sleep-specific oscillatory brain signals characterizing NREM sleep: neocortical slow oscillations, thalamo-cortical spindles and hippocampal SW-Rs (Diekelmann & Born, 2010). The slow (<1 Hz) oscillation is primarily generated in the neocortex (Steriade, 2006; Timofeev & Chauvette, 2011). It spreads across the neocortex and mirrors global synchronous changes of neural activity alternating between periods of increased excitability (depolarized "up-states") and neuronal quiescence (hyperpolarized "down-state"). Furthermore, slow oscillations affect activity in other brain structures, such as the striatum, locus coeruleus and the hippocampus, potentially coordinating communication between these brain regions and the neocortex (Genzel, Kroes, Dresler, & Battaglia, 2014). During NREM sleep stage 2, single slow oscillations might occur as K-complexes which are internally generated but can also be triggered by sensory stimulation during sleep (Colrain, 2005).