Sleep Medicine Reviews 18 (2014) 531–541

Contents lists available at ScienceDirect

Sleep Medicine Reviews

journal homepage: www.elsevier.com/locate/smrv

PHYSIOLOGICAL REVIEW

The reorganisation of memory during sleep

Nina Landmann [a,*], Marion Kuhn [a], Hannah Piosczyk [a], Bernd Feige [a], Chiara Baglioni [a], Kai Spiegelhalder [a], Lukas Frase [a], Dieter Riemann [a], Annette Sterr [b], Christoph Nissen [a,*]

[a] Department of Psychiatry and Psychotherapy, University Medical Center Freiburg, Germany
[b] School of Psychology, University of Surrey, UK

ARTICLE INFO

Article history:
Received 2 July 2013
Received in revised form
10 March 2014
Accepted 10 March 2014
Available online 18 March 2014

Keywords:
Sleep
Learning
Memory
Reorganisation
Plasticity

SUMMARY

Sleep after learning promotes the quantitative strengthening of new memories. Less is known about the impact of sleep on the qualitative reorganisation of memory, which is the focus of this review. Studies have shown that, in the declarative system, sleep facilitates the abstraction of rules (schema formation), the integration of knowledge into existing schemas (schema integration) and creativity that requires the disbandment of existing patterns (schema disintegration). Schema formation and integration might primarily benefit from slow wave sleep, whereas the disintegration of a schema might be facilitated by rapid eye movement sleep. In the procedural system, sleep fosters the reorganisation of motor memory. The neural mechanisms of these processes remain to be determined. Notably, emotions have been shown to modulate the sleep-related reorganisation of memories. In the final section of this review, we propose that the sleep-related reorganisation of memories might be particularly relevant for mental disorders. Thus, sleep disruptions might contribute to disturbed memory reorganisation and to the development of mental disorders. Therefore, sleep-related interventions might modulate the reorganisation of memories and provide new inroads into treatment.

Introduction

Learning, memory and the neural plasticity underlying these processes are fundamental characteristics of animals and humans that allow for adaptation in changing environments. Research over the past years has shown that sleep after learning facilitates the *quantitative strengthening* of newly encoded and initially instable memory traces (for review, please refer to [1]). Quantitative strengthening refers to the veridical preservation of stored information and stabilises memories against disruptive interference and decay [2].

More recently, it has been proposed that sleep might also promote the *qualitative reorganisation* of memories; i.e., the emergence of new memory content that has not been directly learned. This reorganisation of memories during sleep will be the focus of the current review.

A comprehensive model of sleep and memory was recently proposed [3]. This model overarches the entire fate of a novel memory trace from selectivity in initial processing to its subsequent strengthening and further memory evolution; these processes may, at least partially, be interlinked and complementary. The present review elaborates on memory evolution in the form of qualitative changes in memory content rather than the earlier steps of initial processing or strengthening.

Specifically, we review and integrate the current literature related to the two major memory systems, the declarative and the procedural motor systems, from a behavioural perspective. Subsequently, we review the potential neural mechanisms underlying these systems and the modulation of memory reorganisation by emotions. In the final translational section, the potential implications of sleep-related memory reorganisation for the aetiology and treatment of mental disorders are discussed.

Memory reorganisation – the concept

Human memory is an adaptive system. We do not only consolidate experiences as literal records of the past, but we also transform those experiences into new representations that might substantially differ from what was originally encoded [4]. To the best of our knowledge, Sir Frederic Bartlett was the first to

Abbreviations: NREM sleep, non-rapid eye movement sleep; PTSD, post-traumatic stress disorder; REM sleep, rapid eye movement sleep; SWS, slow wave sleep.

* Corresponding authors. Department of Psychiatry and Psychotherapy, University Medical Center Freiburg, Hauptstr. 5, 79104 Freiburg, Germany. Tel.: +49 761 270 65010; fax: +49 761 270 69190.
E-mail addresses: nina.landmann@uniklinik-freiburg.de (N. Landmann), christoph.nissen@uniklinik-freiburg.de (C. Nissen).

http://dx.doi.org/10.1016/j.smrv.2014.03.005
1087-0792/

Glossary of terms

Memory reorganisation	changes in memory content that are reflected by qualitatively new memories that have not been directly learned
Memory strengthening	the veridical preservation of stored information
Schema	mental framework for the organisation and understanding of information that enables the extraction of rules or general concepts on the meta-level

systematically show that memory is constructive in nature [5]. In his famous experiments on repeated reproduction, participants were asked to learn and reproduce a North American folk tale called *The War of the Ghosts*. This tale contains a number of inconsistencies that are puzzling for participants with European socialisations. For example, the text 'One night, two young men from Egulac went down to the river to *hunt seals*, […]' was frequently transformed and normalised to '[…] went down to the river to *go fishing*, […]' in the participants' reconstructions. Bartlett's pioneering findings demonstrated that text reproductions are often inaccurate and primarily represent modified versions (i.e., reorganisations) of the original text in which unusual aspects are altered into more typical scenarios.

These findings led Bartlett to introduce the concept of *schema* as a framework for the organisation and understanding of information [5]. Specifically, schemas capture the ability to systematically organise a multitude of facts and experiences and to extract the general gist which enables the transfer of pre-existing knowledge to novel stimuli and situations. For example, the schema '*dog*' allows for differentiating this species from others, such as cats. Other examples of the constructive nature of memory include observations of erroneous autobiographical memories [6], inconsistencies in eyewitness testimonies [7], and memory distortions in patients with mental disorders [8].

In the following sections, we review and discuss the role of sleep in the reorganisation of memories. We focus on findings from human research and the behavioural perspective of reorganisation. Subsequently, we provide some thoughts on the potential neural mechanisms of this reorganisation. We first discuss memory reorganisation in the declarative system and then discuss reorganisation in the motor system. Studies that comprise both declarative and procedural components are arranged according to their main outcome parameter (Table 1).

The reorganisation of declarative memory during sleep

Declarative memory refers to the memory of events and facts. Declarative memory is believed to emerge from synaptic long-term plasticity in a hippocampal–neocortical network [9]. Based on our integration of the literature, we propose a multi-process model comprising *schema formation*, *schema integration* and *schema disintegration* (Fig. 1). More specifically, *schema formation* arises from the extraction of rules. These rules can then be generalised to novel situations. *Schema integration* pertains to the integration of recent and remote memories, relational memory and the emergence of false memories. *Schema disintegration* describes the process of disbanding existing schemas to allow 'outside the box thinking' and creativity. These schema processes might be associated with distinct sleep characteristics; schema formation and integration might predominantly rely on slow wave sleep (SWS) during non-rapid eye movement (NREM) sleep, whereas schema disintegration might primarily relate to rapid eye movement (REM) sleep. Evidence for and the limitations of these concepts are discussed in the following sections.

Table 1
The reorganisation of memory in the declarative and motor memory system.

Declarative memory
Schema formation
Extraction of rules
Generalisation
Schema integration
Integration of recent and remote memories
Relational memory
False memory formation
Schema disintegration
Associative thinking
Creativity
Motor memory
Movement automatisation
Motor schema
Implicit extraction of rules
Generalisation

Schema formation

Out of a multitude of single pieces of information, a novel schema may emerge. For example, children learn to identify a dog as a dog after having seen many different dogs. As a result, a novel level of information processing in form of the extraction of rules and generalisation might occur. This process has recently been referred to as multi-item generalisation, and sleep plays an important role in this process [3].

Extraction of rules

A pioneering demonstration of the impact of sleep on the extraction of rules was provided by Wagner and colleagues [10]. Using a declarative number reduction task with an embedded deterministic rule, the authors showed that the number of subjects who were able to extract the hidden rule doubled after a night of sleep compared to sleep deprivation or daytime wakefulness of equal duration. However, sleep was not necessary for all participants; some also extracted the rule without sleep, or even directly without the need for prolonged incubation.

The facilitation of rule-extraction during sleep has been replicated in other studies [11,12]. Pace-Schott and colleagues [11] replicated this facilitation using the Iowa Gambling Task, which contains complex probabilistic rules. In contrast to the study on deterministic rule learning by Wagner and colleagues [10] in which some of the participants also extracted the hidden rule without sleep, the participants in the study by Pace-Schott and colleagues benefited from the post-training interval only if that interval was spent sleeping. However, it remains unclear whether this effect is due to an active (i.e., sleep-specific brain activity) or passive (i.e., reduction of interference) effect of sleep. Indirect evidence for a sleep-specific effect has been provided by studies that have reported that rule-extraction is correlated with SWS [13–16] and increases in EEG activity in the 8–12 Hz frequency band [17]. Accordingly, Wilhelm and colleagues [16] showed that the benefit of sleep for explicit rule extraction is greater in children than in adults, and this effect may be a result from the greater amounts of SWS that occur during earlier periods of development.

Some studies have reported that the extraction of explicit rule-knowledge develops immediately after sleep [18,19]. Other studies have reported that sleep only has a priming effect on the capacity for rule-extraction; i.e., knowledge about the hidden rule is not immediately available after sleep but rather requires further