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Review

Sleep and memory in mammals, birds and invertebrates

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ABSTRACT

Sleep supports memory consolidation. Based on studies in mammals, sleep-dependent consolidation has been conceptualized as 'active system consolidation'. During waking, information is encoded into an initial store (hippocampus). During subsequent sleep, some of the newly encoded memories are selected to be reactivated and redistributed toward networks serving as long-term store (e.g., neocortex), whereby memories become transformed into more general, schema-like representations. Here we asked whether sleep in non-mammalian species might play a comparable role for memory. The literature review revealed that sleep produces enhancing effects on memory in all non-mammalian species studied. Furthermore, across species some of the hallmarking features of active system consolidation were identified: Studies of filial imprinting in chicks suggest that a redistribution of imprinting memory toward long-term storage sites occurs during sleep; song learning in birds appears to be driven by reactivations of song representations during sleep; studies of bees demonstrated the selectivity of sleep-dependent consolidation, benefiting extinction but not original classical conditioning. Although overall fragmentary, first evidence in non-mammalian species suggests active system consolidation might be an evolutionary conserved function of sleep.

Contents

Abbreviations: SWS, slow wave sleep; SWA, slow wave activity; REM sleep, rapid eye movement sleep; NonREM sleep, non-rapid eye movement sleep; EEG, electroencephalography; fMRI, functional magnetic resonance imaging; IMM, intermediate and medial mesopallium; RA, robust nucleus of arcopallium; NCL, nidopallium caudolaterale; NCM, caudomedial nidopallium; HVC, a letter based name for a premotor association region in the songbird brain.

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1. Introduction

Learning is tiring! While everyone would agree from his own experience, research confirms a strong link between learning, memory and sleep (Diekelmann and Born, 2010; Rasch and Born, 2013; Stickgold, 2005). Over the last two decades the search for the function of sleep has expanded from the almost exclusive study of mammals to birds and invertebrates, most extensively in respect to work with *Drosophila* (Bushey and Cirelli, 2011). Still the field of sleep research is divided based on the model organisms used: (i) mammals (humans and rodents), (2) birds (chicks, zebra finches and starlings), and (3) fish and invertebrates (Zebrafish, honey bees, *Drosophila* and *Caenorhabditis elegans*). While all of these models have their own strong advantages, little work has been presented extracting the shared features and possible common functions of sleep among these models. Here we review findings in respect to the memory function of sleep in the named models. We will start with a short introduction into the concepts and knowledge about the function of sleep that has been collected from the work with humans and rodents, and then ask whether in birds and invertebrates sleep might play a comparable role for memory.

2. Sleep and memory in mammals

Memory is typically divided into three fundamentally different sub-processes: encoding, consolidation and retrieval. (I) Encoding refers to the up-take of the information to be stored into a neural representation. (II) Consolidation refers to some kind of stabilization of the memory that follows encoding and enables the retention of a memory over time. In the absence of such consolidation the information would be rapidly forgotten. Forgetting can result from a decay of the memory trace or from retroactive interference as the encoding of new information leads to an overwriting of the information encoded before. (III) Retrieval of the stored information refers to the reactivation of a stored memory in the context of more or less goal-directed behavior. Above all, sleep appears to support the consolidation of memory. However, sleep is also known to benefit the subsequent encoding of new information (Tononi and Cirelli, 2014). This second function of sleep will not be covered here.

That sleep supports memory consolidation is known for more than a century. Experimental demonstrations of this effect go back to Heine (1914), a student of Ebbinghaus, and Jenkins and Dallenbach (1924). The latter researchers basically showed that when subjects slept after learning a list of nonsense syllables (encoding), they were able to recall more of the nonsense syllables at a later retrieval test than when they had stayed awake during the retention interval following learning. Since then, numerous other studies, mostly performed in humans, confirmed the benefitting effect of sleep on the retention of different kinds of memory materials and tasks. This research has been in depth reviewed in several recent publications (Abel et al., 2013; Conte and Ficca, 2013; Diekelmann and Born, 2010; Fogel and Smith, 2011; Huber and Born, 2014; Inostroza and Born, 2013; Lewis and Durrant, 2011; Rasch and Born, 2013; Ribeiro, 2012; Stickgold, 2013; Stickgold and Walker, 2013; Wilhelm et al., 2012b). Rather than reiterating these previous reviews, here we want to accentuate several features that appear to hallmark the consolidation process during sleep.

2.1. Sleep-dependent memory consolidation is selective

Hundreds of studies demonstrate a beneficial effect of post-encoding sleep on the consolidation of different types of memory whereas less than a handful of studies claim an opposite effect. However, sleep does not equally benefit all newly encoded representations. Sleep appears to preferentially enhance memories involving the prefrontal–hippocampal memory system during encoding. In rats, sleep affects context conditioning, a hippocampal dependent task, while it does not affect cued conditioning, which is not hippocampus dependent. Five hours of sleep deprivation after context fear conditioning (i.e., learning that a certain surrounding is dangerous) impaired the fear response at a later retrieval test, whereas cued fear conditioning (i.e., learning that a certain tone is followed by a shock independent of the surrounding) was not affected by sleep deprivation (Graves et al., 2003). In two other studies in rats, an object-place recognition task, a temporal order memory task and an episodic-like memory task benefited from post-encoding sleep whereas a novel-object recognition task did not (Inostroza et al., 2013; Oyanedel et al., 2014). Indeed, novel-object recognition in these studies was the only task that does not critically depend on intact hippocampal function (Bussey et al., 2000; Mumby et al., 2002).

Also in humans, sleep seems to preferentially help consolidate hippocampus-dependent memory (e.g., contextual types of memory) rather than hippocampus-independent memory (e.g., item memory) (Aly and Moscovitch, 2010; Rauchs et al., 2004; van der Helm et al., 2011; Weber et al., 2014). Memory for the spatio-temporal context of an episode critically depends on hippocampal function, whereas item memory, like object recognition memory, does not (Davachi, 2006; Eichenbaum et al., 2007). For example, when participants learned lists of words (item memory) while facing two different posters (contexts), napping following learning led to better memory for the posters but not for the list words compared with a no-nap control condition. Recognition of the list words does not critically depend on hippocampal function (van der Helm et al., 2011). Other studies likewise revealed selectively improving effects of sleep on spatio-temporal context memory (Griessenberger et al., 2012; Rauchs et al., 2004; Wilhelm et al., 2011b), and also showed that such enhancing effects on context can be blocked by the administration of glucocorticoids during retention sleep, which affect in particular hippocampal circuits (Griessenberger et al., 2012; Kelemen et al., 2014; Wilhelm et al., 2011b).

In humans hippocampus-dependent memory is traditionally equated with declarative memory which refers to memory for episodes and facts, and is explicitly (i.e., consciously) encoded and retrieved (Squire and Zola, 1996). Procedural memory for perceptual and motor skills, in contrast, is thought of not essentially relying on hippocampal function. However, more recent imaging studies revealed that learning of such procedural tasks entailing a sequential feature, at least in the initial stages of training, typically also involves hippocampal function (Henke, 2010; Schendan et al., 2003). Regarding sleep-dependent consolidation, the hippocampal involvement at training, specifically the functional connectivity between hippocampus and prefrontal areas, appears to even predict the overnight gain in skill (Albouy et al., 2008, 2013a,b). Also, the involvement of the prefrontal–hippocampal system in procedural learning is enhanced when the training takes place under