Neurobiology of Learning and Memory xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Neurobiology of Learning and Memory

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

The transformation of multi-sensory experiences into memories during sleep

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ARTICLE INFO

Keywords:
Sleep
Memory consolidation
Hippocampus
Cortex
Sharp wave ripples
Sensory processing
Reactivation
Replay

ABSTRACT

Our everyday lives present us with a continuous stream of multi-modal sensory inputs. While most of this information is soon forgotten, sensory information associated with salient experiences can leave long-lasting memories in our minds. Extensive human and animal research has established that the hippocampus is critically involved in this process of memory formation and consolidation. However, the underlying mechanistic details are still only partially understood. Specifically, the hippocampus has often been suggested to encode information during experience, temporarily store it, and gradually transfer this information to the cortex during sleep. In rodents, ample evidence has supported this notion in the context of spatial memory, yet whether this process adequately describes the consolidation of multi-sensory experiences into memories is unclear. Here, focusing on rodent studies, I examine how multi-sensory experiences are consolidated into long term memories by hippocampal and cortical circuits during sleep. I propose that in contrast to the classical model of memory consolidation, the cortex is a "fast learner" that has a rapid and instructive role in shaping hippocampal-dependent memory consolidation. The proposed model may offer mechanistic insight into memory biasing using sensory cues during sleep.

1. Introduction

Sleep benefits memory (Diekelmann & Born, 2010; Walker & Stickgold, 2004). For example, sleep improves the formation of motor skill memories (Fischer, Hallschmid, Elsner, & Born, 2002; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002) and performance on visual discrimination tasks (Mednick et al., 2002; Stickgold, James, & Hobson, 2000). Hippocampal-dependent declarative memories have also been shown to benefit from sleep (Marshall & Born, 2007), as evidenced by improved performance on paired-associate lists (Plihal & Born, 1997), as well as performance on memory of vocabulary (Gais & Born, 2004; Gais, Lucas, & Born, 2006; Gais, Rasch, Wagner, & Born, 2008) after sleep. While it is clear that sleep is important for memory, the quest to understand the precise neural mechanisms of memory consolidation during sleep is still ongoing.

2. The Two-Stage Model for consolidation of spatial information

Classical clinical cases still provide some of the clearest evidence for the involvement of the hippocampus and cortex in memory consolidation. The finding that following hippocampal lesions, patient Henry Molaison (H.M.) lost the ability to form new declarative memories while retaining memories from his childhood (Scoville & Milner, 1957) has promoted the idea that memories are temporarily stored in the hippocampus and then subsequently transferred to the cortex for long term storage (McClelland, McNaughton, & O'Reilly, 1995). Indeed, the hippocampus is often considered to be a "fast learner", encoding information during experience and then "teaching" the cortex, the "slow learner", during sleep (Battaglia, Benchenane, Sirota, Pennartz, & Wiener, 2011; Frankland & Bontempi, 2005; Lisman & Morris, 2001; McClelland et al., 1995; O'Reilly & Rudy, 2000). This account has received substantial support from research in rodents, where neurophysiological phenomena that appear consistent with this process have been identified (Buzsaki, 1989, 1996, 1998, 2015).

One of the most influential and constructive models of system-level memory consolidation that was based on identified neurophysiological processes in the hippocampus is the Two-Stage Model (Buzsaki, 1989, 1996, 1998, 2015). According to this model, the first stage occurs during behavior, when the hippocampus rapidly encodes and temporarily stores various aspects of the experience. In the second stage, which occurs during sleep or awake quiescence, the newly acquired hippocampal information is repeatedly replayed and communicated to the cortex, driving cortical plasticity and allowing for the longer-term storage of the memory.

The encoding and reactivation stages described by this model are most intuitive, and are supported by extensive evidence, in the context of spatial coding in rodents. As rodents traverse their environment, the physical location of the animal is encoded via the activity of hippocampal place cells (O'Keefe, 1976; O'Keefe & Dostrovsky, 1971). Cells in area CA1 of the hippocampus typically fire action potentials whenever

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https://doi.org/10.1016/j.nlm.2018.03.019
Received 13 December 2017; Received in revised form 11 March 2018; Accepted 23 March 2018
1074-7427/ © 2018 Published by Elsevier Inc.

the animal is in a specific location within its environment (i.e., the cell's place field). At the neural population level, the animal's movement along a trajectory in its environment is coded by a temporal sequence of spiking activity of place cells with place fields located along the trajectory path (Frank, Brown, & Wilson, 2000; Wikenheiser & Redish, 2012, 2015a, 2015b). When the animal is immobile, a distinct hippocampal circuit encodes its position (Kay et al., 2016). The hippocampus thus maintains a continuous representation of the current location of the animal. An important principle of the Two-Stage Model is that beyond this momentary, "online", representation of the animal's current location, neural activity evoked during navigation leaves a synaptic memory trace in the hippocampus that allows temporary storage of the experience (Buzsaki, 1989, 1996, 2015).

There is also convincing evidence for the second, reactivation stage, of the Two-Stage Model in the context of spatial coding. During the "offline" states of non-rapid eye movement (nREM) sleep and awake quiescence, the hippocampus exhibits strong bursts of neural population activity. In the CA1 region of the hippocampus, these events can be detected as strong deflections in the local field potential (LFP) (the "sharp wave") and a simultaneous fast (150–250 Hz) oscillation (the "ripple"), together named sharp wave ripples (SWRs). SWRs originate in the hippocampal area CA3 (Buzsaki, Leung, & Vanderwolf, 1983; Sullivan et al., 2011) and their generation is believed to be the result of excitatory recurrent interconnectivity in this area. The duration of a single SWR is on the order of 100 ms, and during nREM sleep SWRs typically occur every 0.5–3 s (Csicsvari, Hirase, Czurko, Mamiya, & Buzsaki, 1999a, 1999b; Eschenko, Ramadan, Molle, Born, & Sara, 2008; Girardeau, Benchenane, Wiener, Buzsaki, & Zugaro, 2009; Sullivan et al., 2011; Wiegand et al., 2016). A number of features make SWRs an attractive candidate mechanism of memory consolidation. First, the identity and timing of CA1 cell firing within a single SWR is not random. Rather, the firing sequences of place cells that occurred during recent movement trajectories are reactivated during single SWRs in a time-compressed manner, a striking phenomenon named "replay" (Diba & Buzsaki, 2007; Foster, 2017; Skaggs & McNaughton, 1996; Wilson & McNaughton, 1994). Thus, the replay firing patterns in CA1 during SWRs fulfill a basic requirement of a consolidation mechanism, namely reactivation of the representation of a previous experience in the absence of sensory cues. Furthermore, reactivated hippocampal representations engage cortical networks, as SWRs can drive excitatory responses in cortical output regions (Chrobak & Buzsaki, 1996; Isomura et al., 2006). Finally, studies have established a causal role for SWRs in learning: SWR rates increase in post-learning sleep (Eschenko et al., 2008), and disruption of hippocampal SWRs impedes learning (Ego-Stengel & Wilson, 2010; Girardeau et al., 2009; Jadhav, Kemere, German, & Frank, 2012). Taken together, these findings support the idea that SWRs facilitate repeated transmission of representations of recent experiences from the hippocampus to the cortex, potentially inducing synaptic changes that would support long-term memory storage (Buzsaki, 1996, 1998, 2015; Diekelmann & Born, 2010; Inostroza & Born, 2013; Molle & Born, 2009).

3. The rodent hippocampus and non-spatial information

A key component of this model is the hippocampus functioning as a temporary information storage unit from the time of experience and until consolidation is complete. In the context of spatial coding, this buffering capacity may be achieved by rapid hippocampal synaptic plasticity occurring during experience as a result of place cell activity. This synaptic plasticity may contribute to the formation of hippocampal ensembles that subsequently tend to co-fire during hippocampal SWRs in sleep, potentially driving slower synaptic changes in the cortex (Buzsaki, 1989, 1996, 1998).

However, while the Two-Stage Model provides an elegant description for encoding and reactivation of spatial information, real-life experiences and the resulting episodic memories are often multi-sensory. The spatial component of an experience often coexists with, and is sometimes dominated by, visual, auditory, somatosensory, olfactory and gustatory cues. In humans, there is overwhelming evidence that the hippocampus is involved in consolidation of both spatial and non-spatial aspects of declarative memories (Squire, Stark, & Clark, 2004). In rodents, hippocampal involvement in consolidation of spatial aspects of memory are well-established (O'Keefe & Nadel, 1978) and while a matter of some dispute (Eichenbaum, Dudchenko, Wood, Shapiro, & Tanila, 1999; O'Keefe, 1999), a growing body of evidence implicates the hippocampus in consolidation of non-spatial memories, including contextual fear memory (Anagnostaras, Maren, & Fanselow, 1999; Kim & Fanselow, 1992), trace conditioning (Kim, Clark, & Thompson, 1995; McEchron, Bouwmeester, Tseng, Weiss, & Disterhoft, 1998; Weiss, Bouwmeester, Power, & Disterhoft, 1999), recognition memory (Broadbent, Squire, & Clark, 2004; Clark, Zola, & Squire, 2000; Cohen et al., 2013; Fortin, Wright, & Eichenbaum, 2004; Langston & Wood, 2010) (although recognition of object-in-place may be especially dependent on the hippocampus (Oliveira, Hawk, Abel, & Havekes, 2010; Winters, Forwood, Cowell, Saksida, & Bussey, 2004)), temporal order of events (Fortin, Agster, & Eichenbaum, 2002; Kesner, Gilbert, & Barua, 2002), social transmission of food preference (Clark, Broadbent, Zola, & Squire, 2002; Winocur, 1990) and memory of delay timing (Clark, West, Zola, & Squire, 2001).

4. The Two-Stage Model for non-spatial memories

How is the hippocampus involved in memory consolidation of non-spatial information? Revisiting the Two-Stage Model, one parsimonious possibility is that the hippocampus encodes and reactivates non-spatial information in the same way as with spatial information. Under this view, the hippocampus encodes and temporarily stores multi-sensory information during experience, and then reactivates and transmits this information to the cortex in the second stage during sleep. In support of this alternative, studies have shown non-spatial coding in the hippocampus during experience (Wood, Dudchenko, & Eichenbaum, 1999). For example, hippocampus has been shown to encode timing aspects of a task (Eichenbaum, 2014; Pastalkova, Itskov, Amarasingham, & Buzsaki, 2008), the presence of objects or environmental features (Deshmukh & Knierim, 2013; Komorowski, Manns, & Eichenbaum, 2009; Leutgeb et al., 2005; O'Keefe, 1976; Singer & Frank, 2009), movement trajectory (Ainge, Tamosiunaite, Woergoetter, & Dudchenko, 2007; Frank et al., 2000; Grieves, Wood, & Dudchenko, 2016; Hollup, Molden, Donnett, Moser, & Moser, 2001; Knierim, Kudrimoti, & McNaughton, 1995), novelty (Cheng & Frank, 2008; Larkin, Lykken, Tye, Wickelgren, & Frank, 2014), and mixtures of behavioral parameters (McKenzie et al., 2014). In some cases hippocampal activity can be modulated by sensory cues during experience (Igarashi, Lu, Colgin, Moser, & Moser, 2014; Itskov, Vinnik, & Diamond, 2011; Itskov, Vinnik, Honey, Schnupp, & Diamond, 2012; Moita, Rosis, Zhou, LeDoux, & Blair, 2003).

However, the rodent hippocampus seems to lack the ability to reliably store the rich and highly detailed sensory information that makes up real-life experiences. For example, cells in hippocampal area CA1 of the rat encode the presence of another rat, but do not discriminate its identity from other rats (von Heimendahl, Rao, & Brecht, 2012). In a task where sound identity indicated the location of the next reward, some cells showed selective sound responses, but the prevalence of these cells was near chance levels (17/199, 8.5%) (Bendor & Wilson, 2012). In the olfactory domain, some hippocampal cells were found to be active during odor sampling, but their firing represented the valence and behavioral relevance of the odors, and not odor identity (Eichenbaum, Kuperstein, Fagan, & Nagode, 1987; Otto & Eichenbaum, 1992). In a study where rabbits were presented with stimuli of different modalities, many hippocampal neurons in CA3 showed responses during stimulation, but these responses were not selective to specific stimuli within a modality, and even to stimuli across modalities

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