



Review

The function of the sleep spindle: A physiological index of intelligence and a mechanism for sleep-dependent memory consolidation

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ABSTRACT

Until recently, the electrophysiological mechanisms involved in strengthening new memories into a more permanent form during sleep have been largely unknown. The sleep spindle is an event in the electroencephalogram (EEG) characterizing Stage 2 sleep. Sleep spindles may reflect, at the electrophysiological level, an ideal mechanism for inducing long-term synaptic changes in the neocortex. Recent evidence suggests the spindle is highly correlated with tests of intellectual ability (e.g.; IQ tests) and may serve as a physiological index of intelligence. Further, spindles increase in number and duration in sleep following new learning and are correlated with performance improvements. Spindle density and sigma (14–16 Hz) spectral power have been found to be positively correlated with performance following a daytime nap, and animal studies suggest the spindle is involved in a hippocampal–neocortical dialogue necessary for memory consolidation. The findings reviewed here collectively provide a compelling body of evidence that the function of the sleep spindle is related to intellectual ability and memory consolidation.

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1. Introduction

What mechanisms are involved in the process of consolidating newly learned information into a more stable form of long-term memory? Sleep has been identified as one of the biological states necessary for efficient memory consolidation; the process of transforming a newly acquired, labile memory into an endur-

ing long-term memory. A compelling body of research exists from both human (Smith, 1985, 1995; Stickgold and Walker, 2007) and animal studies (Hennevin et al., 1995; Smith, 2003) establishing a link between rapid eye movement (REM) sleep and memory. Despite this, an ongoing (and sometimes heated) debate continues about the many functions of sleep (Brawn et al., 2010; Maquet, 2001; Rickard et al., 2008; Siegel, 2001; Stickgold and Walker, 2005; Vertes and Siegel, 2005).

More recently, non-REM sleep has been implicated in the consolidation of new learning as well (Buzsáki, 1984, 1989; Gais and Born, 2004; Nader and Smith, 2003; Smith and MacNeill, 1994). Here we summarize recent evidence which suggests that the sleep spindle – an electroencephalographic (EEG) event that characterizes and predominates non-REM sleep – reflects, at the electrophysiological level, a mechanism involved in the consolidation of memory during sleep. Moreover, it appears that native sleep spindles reflect intellectual ability as measured by aptitude batteries including intelligence quotient (IQ) tests, and may serve as a physiological index of intelligence. We propose that baseline inter-individual differences in sleep spindles are correlated with learning potential. On the other hand, we suggest that learning-related increases in sleep spindles reflect processes specific to memory consolidation and may involve different neural substrates. Furthermore, we suggest that important dissociations between sleep states and memory systems have been identified in humans (Fogel et al., 2007b; Plihal and Born, 1997). For example, REM sleep appears to be involved in procedural learning that is cognitively complex and involves the acquisition of new rules (Fogel et al., 2007b; Plihal and Born, 1997; Smith et al., 2004b), whereas Stage 2 sleep is involved in procedural learning that involves the refinement of existing skills (Fogel et al., 2007b). Recent findings in animals suggest learning-related increases in sleep spindles may indicate one step in a series of sequential steps of sleep-dependent memory consolidation processes during non-REM sleep that follow previously identified learning-related changes in REM sleep (originally suggested by Buzsáki, 1984, 1989; for review see Smith, 1985; and for more recent findings Fogel et al., 2009). Before describing evidence implicating sleep spindles in memory consolidation and their relation to IQ, it is necessary to describe the memory systems and memory processes involved (Section 2), followed by a brief overview of sleep–wake states (Section 3) and factors related to sleep spindles (Section 4). This is not intended to be a comprehensive review of memory systems, nor sleep–wake states, but should provide adequate background for the reader to understand the role of the sleep spindle in intellectual ability (Section 5) and memory consolidation (Sections 6–9). Finally, we provide important future directions (Section 10) which we hope will lead us to a better understanding of the processes involved in sleep-related synaptic plasticity and memory consolidation.

2. Memory systems and memory consolidation processes

2.1. Declarative memory

Human long-term memory is not dependent on a unitary system of brain structures and mechanisms and can be subdivided into a number of subtypes. Declarative memory has traditionally been subdivided into episodic and semantic memory. The paired associates task is one task commonly used to study declarative learning that is explicitly learned. In this task, pairs of words (or pictures) are visually presented, where the goal is to explicitly memorize the word pairs by either rehearsal, or some other mnemonic strategy. This type of learning involves the hippocampus, and is impaired in patients with medial temporal lobe damage (Scoville and Milner, 1957; Warrington, 1996). Declarative memory is generally considered memory for learning and knowing “*what*” as opposed to “*how*”.

The taxonomy of memory has been extensively researched at both the cognitive and behavioral level and many of the associated brain structures have been localized by means of imaging techniques (Doyon et al., 2003; Schacter, 1997). Newly learned memory traces are initially in a labile form, and the process of forming a stable and lasting memory requires long periods of post acquisition time ranging from hours to years (Haist et al., 2001; Kim and Fanselow, 1992; Korman et al., 2007; Mednick et al., 2003; Scoville and Milner, 1957; Zola-Morgan et al., 1992). Generally defined, memory consolidation is the process by which newly acquired, labile memories are transformed into more stable, permanent long-term memories. This process is thought to primarily involve brain structures such as the hippocampus and the thalamus. Over the course of declarative memory consolidation, the influence of the hippocampus and/or the thalamus diminishes until the memory is permanently stored in the neocortex (Dudai and Eisenberg, 2004; Frankland et al., 2004). It is not yet entirely clear which physiological mechanisms are involved in declarative memory consolidation, especially with regards to memory processes exclusive to sleep. However, recent evidence suggests that certain features of sleep appear to be linked to memory consolidation processes such as slow wave activity (Möller et al., 2002), hippocampal sharp waves (Buzsáki, 1984), ripples (Möller et al., 2009) theta activity (Fogel et al., 2007b), rapid eye movements during REM sleep (De Koninck et al., 1989; Fogel et al., 2007b; Smith and Lapp, 1991), sleep spindles in humans (e.g., Fogel and Smith, 2006; Gais et al., 2002; Schabus et al., 2004; Clemens et al., 2005) and for spatial memory and avoidance learning in animals (Fogel et al., 2009; Möller et al., 2009; Schiffelholz and Aldenhoff, 2002). For a recent review see Diekelmann and Born (2010).

2.2. Procedural memory

Procedural memory is generally considered memory for learning and knowing “*how*” as opposed to “*what*”. Non-declarative memory can be subdivided into procedural (skills and habits), classical conditioning, priming and non-associative learning (Gabrieli, 1998; Milner et al., 1998; Squire and Zola, 1998). Procedural memory can be further subdivided depending on the cognitive complexity, or novelty of the task. For example, procedural memory is usually further subdivided (and especially so in the sleep and memory literature) into motor (or simple) procedural memory, and cognitive (or complex) procedural memory. For example, the pursuit rotor (Grafton et al., 1992) and the finger tapping task (Ungerleider et al., 2002) have been classified as a simple motor procedural memory task that involve the refinement of skills and habits (usually motor skills) for which there is an already pre-existing set of skills to learn the task. On the other hand, the artificial grammar task (Cleemans and McClelland, 1991; Fischer et al., 2006), Tower of Hanoi and the mirror tracing task have been classified as complex cognitive procedural memory tasks (Fogel et al., 2007b; Smith, 1995, 2001), however, other terminology is commonly used to describe the same types of tasks (Gabrieli, 1998). Complex cognitive procedural learning involves the understanding of new rules or the acquisition of entirely new skills in order to improve performance (for review see Smith, 1995, 2001; and Smith et al., 2004a for a more recent formulation of these ideas).

Interestingly, procedural memory is largely spared in amnesia resulting from damage to the medial temporal lobe. Procedural memory is dependent on a variety of structures such as the striatum, cerebellum, pons, globus pallidus and cortical regions that are independent of the hippocampus (Doyon et al., 2003; Schacter, 1997). The compartmentalization of the types of procedural memory to different brain structures suggests that there may be separate mechanisms for consolidating various subtypes of memory. Proce-

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