



Age-related differences in sleep-based memory consolidation: A meta-analysis



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ABSTRACT

A period of post-learning sleep benefits memory consolidation compared with an equal-length wake interval. However, whether this sleep-based memory consolidation changes as a function of age remains controversial. Here we report a meta-analysis that investigates the age differences in the sleep-based memory consolidation in two types of memory: declarative memory and procedural memory. The meta-analysis included 22 comparisons of the performance between young adults ($N = 640$) and older adults ($N = 529$) on behavioral tasks measuring sleep-based memory consolidation. Our results showed a significant overall sleep-based beneficial effect in young adults but not in older adults. However, further analyses suggested that the age differences were mainly manifested in sleep-based declarative memory consolidation but not in procedural memory consolidation. We discussed the possible underlying mechanisms for the age-related degradation in sleep-based memory consolidation. Further research is needed to determine the crucial components for sleep-related memory consolidation in older adults such as age-related changes in neurobiological and cardiovascular functions, which may play an important role in this context and have the potential to delineate the interrelationships between age-related changes in sleep and memory.

1. Introduction

1.1. Sleep-based memory consolidation

Sleep plays an important role in memory consolidation. Jenkins and Dallenbach were amongst the first to provide experimental evidence for the beneficial effect of sleep on memory consolidation (Jenkins and Dallenbach, 1924). More recently, accumulating evidence suggest that sleep, compared to an equivalent period of wakefulness, promotes memory consolidation (e.g., Diekelmann, 2014; Rasch and Born, 2013; Stickgold and Walker, 2005; Walker, 2009). These benefits of sleep, rather than wakefulness, on memory preservation reflect the effect of sleep-based memory consolidation.

The sleep-based memory consolidation effect is generally measured by comparing a sleep condition with a wake condition in a typical experimental design. In the sleep condition, participants take part in the learning session in the evening, and perform the memory retest in the following morning after a night of sleep. In contrast, in the wake condition, participants take part in the learning session in the morning,

and perform the memory retest in the evening after an equivalent interval of wakefulness (Fig. 1A). While consolidation can occur over intervals of wakefulness, it is optimized over sleep in healthy young adults (e.g., Doyon et al., 2009; Fischer et al., 2002; Spencer et al., 2006; Walker et al., 2005). Some studies also incorporated a nap paradigm, as napping has been reported to facilitate memory consolidation as well (Fogel et al., 2014; Korman et al., 2015; Lahl et al., 2008; Mednick et al., 2003; Vien et al., 2016).

In addition to the general sleep-based memory consolidation, researchers have further explored how this effect may be implicated in different types of memory, such as declarative memory (Clemens et al., 2005; Ekstrand, 1967; Peigneux et al., 2004; Scullin and McDaniel, 2010) and procedural memory (Antony et al., 2012; Durrant et al., 2011; Fischer et al., 2002; Walker et al., 2002).

On the one hand, declarative memory affords the ability to store information explicitly, so that the information can be consciously retrieved at a later time (Squire, 1996; Tulving, 1985). Word-pair association tasks are typically used to investigate the function of sleep on declarative memory consolidation (Baran et al., 2016; Ekstrand,

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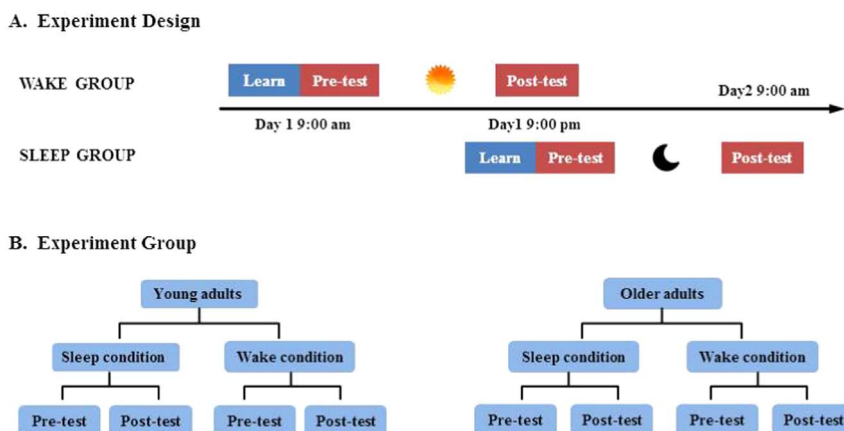


Fig. 1. Experiment design and groups. A. During the learning phase, participants encode the study material and have an immediately recall, after which the sleep group undergo 12-h sleep, whereas the wake group have normal activities; during the testing phase, participants are instructed to have a retest of the material which are learned before; B. In the age-related sleep-based consolidation experiment, there are the sleep condition and the wake condition in both young and older adults, within which pre-test and post-test are administrated respectively.

1967; Lahl et al., 2008; Mander et al., 2013; Wilson et al., 2012). These tasks require the participants to learn a list of word-pairs, and perform cued-recall/recognition tests after an interval of sleep or wakefulness (Backhaus et al., 2007; Mander et al., 2013; Squire and Zola, 1996; Wilson et al., 2012). In addition to word-pair association paradigm, sleep-based declarative memory consolidation has also been observed in other tasks, such as object/face locations, personal event memories, and emotional scenes (Aly and Moscovitch, 2010; Cherdieu et al., 2014; Jones et al., 2016; Payne et al., 2008; Rasch et al., 2007; Scullin and Bliwise, 2015; Scullin and McDaniel, 2010; Talamini et al., 2008; Wagner et al., 2001). Since declarative memory traces are highly susceptible to decay, sleep-based declarative memory consolidation effect is often manifested as a diminished forgetting of materials at the retrieval stage in the sleep condition, relative to the wake condition (Wilson et al., 2012).

On the other hand, procedural memory refers to a heterogeneous collection of abilities that affords the capacity to acquire information implicitly, and is concerned with how things are done (Squire and Zola, 1996; Tulving, 1985). Classic sequence learning tasks are typically used to study the function of sleep on procedural memory consolidation (Bottary et al., 2016; Fogel et al., 2014; Pace-Schott and Spencer, 2013; Tucker et al., 2011; Vien et al., 2016; Walker et al., 2005). The sequence learning task is modified from the serial reaction time task (Nissen and Bullemer, 1987). In a typical sequence learning task, participants are presented with a numeric sequence (e.g., 4-1-3-2-4) throughout the experiment, and are instructed to press a response key that corresponds to the spatial location of the visual stimulus. Similar to declarative memory consolidation, sleep also seemed to facilitate motor sequence consolidation, such as enhancing the speed and accuracy of motor performance in the absence of any overt training during the retention period (Fischer et al., 2002; Karni et al., 1994; Spencer et al., 2006; Walker et al., 2005). However, other studies claimed that whereas sleep may play a protection role in the motor skills consolidation, it did not result in performance enhancement, but rather made the acquired procedural skills more stable and resistant to interference (Cellini and McDevitt, 2015; Doyon et al., 2009; Mednick et al., 2011; Nettersheim et al., 2015; Pan and Rickard, 2015; Rickard et al., 2008). In addition to sequence learning tasks, sleep effects on procedural memory consolidation have also been reported in other motor tasks, including the rotor pursuit task, novel walking task, and mirror tracing task (Al-Sharman and Siengsukon, 2014; Mantua et al., 2015; Peters et al., 2008; Scullin and Bliwise, 2015). In the current meta-analysis, we included a range of behavioral tasks investigating the age differences on sleep-based memory consolidation. These tasks are summarized in Table 1.

1.2. Sleep-based memory consolidation and aging

With increasing age, there are substantial changes to sleep quantity and quality, including changes to slow-wave sleep (SWS), sleep latency, sleep fragmentation, rapid eye movement (REM) density, and sleep spindles (e.g., Espiritu, 2008; Ohayon et al., 2004; Pace-Schott and Spencer, 2011; Vitiello, 2006; Wolkove et al., 2007). In parallel, numerous studies have confirmed that memory function deteriorates in older adults (e.g., Park et al., 2002; Park and Reuter-Lorenz, 2009). The fact that aging is accompanied by changes in both sleep and memory functions leads to an alluring question of whether age-related changes in sleep and memory contribute to a decline of the sleep-based memory consolidation in older adults. In recent decades, a number of behavioral studies have investigated the relationship between sleep-based memory consolidation and aging. However, these studies showed inconsistent results, especially when it comes to different types of memory (e.g., declarative memory and procedural memory).

On the one hand, for declarative memory, although some studies found that older adults benefited from a night of sleep as much as young adults (Aly and Moscovitch, 2010; Sonni and Spencer, 2015; Wilson et al., 2012), other studies showed that these benefits were reduced in older adults (Backhaus et al., 2007; Baran et al., 2016; Cherdieu et al., 2014; Mander et al., 2012, 2013; Scullin, 2013; Varga et al., 2016). On the other hand, with respect to procedural memory, while a number of studies suggested that sleep-based memory consolidation may be preserved with aging (Al-Sharman and Siengsukon, 2014; Backhaus et al., 2015; Gudberg et al., 2015; King et al., 2016; Mantua et al., 2015; Tucker et al., 2011), others indicated that it is impaired (Bottary et al., 2016; Fogel et al., 2014; Pace-Schott and Spencer, 2013; Peters et al., 2008; Spencer et al., 2007, 2006; Vien et al., 2016).

1.3. The present study

Due to the aforementioned inconsistency in previous findings, we aim to use a meta-analytic approach to systematically evaluate existing evidence on the age-related changes in sleep-based memory consolidation. First, we assess the empirical evidence from behavioral studies to quantify age differences in sleep-based memory consolidation. Second, we investigate whether the age-related alterations in sleep-based memory consolidation differ between declarative memory and procedural memory, as these types of memory are measured by different tasks and engage different brain activity. Furthermore, as sleep-based memory consolidation are examined by calculating the difference in memory retention between the sleep and wake conditions, we test the

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