Neuropsychologia 97 (2017) 46–55

Contents lists available at ScienceDirect

Neuropsychologia

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

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

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ARTICLE INFO

Keywords:
Aging
Sleep-based memory consolidation
Declarative memory
Procedural memory
Meta-analysis

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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http://dx.doi.org/10.1016/j.neuropsychologia.2017.02.001
Received 28 October 2016; Received in revised form 22 January 2017; Accepted 1 February 2017
Available online 02 February 2017
0028-3932/

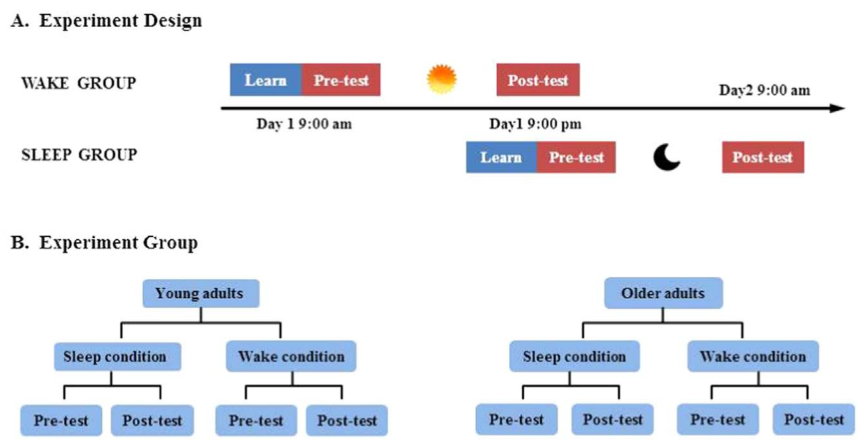

Fig. 1. Experiment design and groups. A. During the learning phase, participants encode the study material and have an immediately recall, after which the sleep group undergo 12-h sleep, whereas the wake group have normal activities; during the testing phase, participants are instructed to have a retest 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

Table 1
Behavioral tasks of sleep-base memory consolidation included in this meta-analysis.

Category	Task	Task description	N
Procedural memory	Sequence learning task	In these tasks, a trial is cued with the presentation of an 'X' in one of the four boxes, participants are instructed to press one of four response keys based on the spatial position of a visual stimulus presented on a computer monitor.	8
	Mirror tracing task	The task required that participants trace a figure on screen using a stylus. Participants were told to stay within the lines of the presented figure. A screen mounted over the hand and iPad occluded direct visual feedback, but the workspace was visible through a mirror that was mounted behind the workspace, providing inverted visual feedback.	1
Declarative memory	Association memory (word pair/ object-location learning task)	In word pair learning, words are randomly paired to created several lists of word pairs (e.g., CAT-COACH, DESK-ICE). Participants are instructed to study each pair of words for subsequent recall/ recognition, and a mnemonic strategy are instructed to use to facilitate learning. While object-location task is similar as word pair learning task, only that use picture pair instead of word pair in the learning phase.	5
	Question list	There is a list of questions to assess personal episodic memories for the conversation the participant has that morning (or the previous evening), as well as memory for the things they have read or seen on the news, radio, or television.	1
	Logical memory	The Logical Memory section of the Wechsler Memory Scale III (WMS-III), which consists of two short-paragraph-length stories. The stories are scored in terms of the number of story units recalled, as specified in the WMS-III scoring protocol.	1
	Emotional picture recognition task	The task contains valence-based pictures (negative, neutral and positive). During encoding, participants view a part of pictures (named old pictures), and rate the valence and arousal for each picture. During recognition, old pictures with new picture are intermixed, participants were again rate their valence and arousal, and further judge whether they have seen each picture by pressing corresponding keyboards.	2

Note: *N*, number of comparisons that used in the respective task included in this meta-analysis.

age effect in the sleep condition and wake condition separately, so as to clarify the origination of the age-related differences in sleep-based memory consolidation. Finally, we explore moderating factors that could be associated with sleep-based memory consolidation.

2. Methods

2.1. Literature search

We identified studies to include in the current meta-analysis in two ways. First, we implemented an initial broad and thorough literature search on PubMed, EBSCO (PsyINFO, PsycARTICLES, PsycCRITIQUES, PsycEXTRA, and PsycTESTS), Web of Science and Google Scholar. We searched for studies published between January 1, 1990 and January 1, 2017. We combined alternative terms for aging and sleep-based memory consolidation in our search. For aging, we used terms including "aging, age-related, elderly, elders, elderly persons, elderly people, older adults, older people, and older persons". For sleep to memory consolidation, we used terms including "sleep-based memory consolidation, sleep-related enhancement, sleep-dependent consolidation, sleep-dependent gains, sleep-dependent improvement, sleep-dependent learning and sleep-dependent retention". Second, we conducted an additional literature search from the references of the included studies, as well as a number of relevant review papers on aging and sleep-based memory consolidation (Diekelmann et al., 2009; Harand et al., 2012; Hornung et al., 2005; Pace-Schott and Spencer, 2011; Scullin and Bliwise, 2015), to identify as many potential studies as possible.

2.2. Inclusion criteria

Of the studies identified from the literature search, we included those that met the following criteria (Fig. 1B): (1) the study included both the experimental sleep condition and the control wake condition; (2) the study reported pre-test and post-test or change values of memory performance for both the sleep condition and wake condition; (3) the study included samples of both healthy young (*ca.* 18–35 years) and older adults (*ca.* 60–85 years); and (4) the study reported statistics comparing the performance from different age groups, such as means, standard deviations, and *t/F* test values that reflect the sleep-based retentions, or other statistical information that can be used to calculate effect sizes. We also contacted authors to request these data if they were not readily available from the published articles.

2.3. Exclusion criteria

On top of the inclusion criteria, we excluded studies from our meta-analysis if they: (1) focused on populations with clinical conditions (e.g., stroke, Parkinson's disease); (2) lacked of young adults sample or the wake condition in their experiment design, since we aimed to compare the age effect on the sleep-based memory consolidation; and (3) were case studies or review articles. Additionally, two studies were excluded because one did not provide enough data to compute effect size (Scullin, 2013), and another applied sleep deprivation as control instead of wakefulness (Tucker et al., 2011).

2.4. Data extraction

Two of the authors (W. Gui and J. Yu) determined whether the studies should be included based on the inclusion and exclusion criteria. Three of the authors coded each study included in the meta-analysis to extract major outcomes (W. Gui, H. Li, and J. Yu). Discrepancies were addressed with discussion.

2.5. Data analysis

To examine the magnitude of the sleep-based memory consolidation effect across all comparisons, we computed a synthesized effect size Cohen' s *d* (Cohen, 1988) with a corresponding confidence interval (CI) of 95%. In addition, we used the homogeneity statistic (Q-test) to test whether the studies included in the meta-analysis shared a common population effect size (Lipsey and Wilson, 2001). Furthermore, we tested publication bias with Egger's regression intercept test. Egger's test is an index of the funnel plot, which can be used to assess publication bias. Significant results of the Egger's test indicate possible publication bias in the data (Egger et al., 1997). These calculations were conducted using the Comprehensive Meta-Analysis 2.0 (CMA) software (http://www.meta-analysis 2.0.com).

To compare the age differences on the sleep-based memory consolidation across memory types, we calculated the effect sizes for the differences between the sleep condition and the wake condition in each age group. First, the memory performance change scores between post-test and pre-test in each condition were calculated respectively; and then the change value was compared between the sleep condition and wake condition. When the mean and standard deviation were not available, the exact *p*-value, *t*-value, or *F*-value was used to achieve the derivation of effect size. The effect size was defined as positive if participants in the sleep condition performed better than those in the wake condition. In addition, we ran a contrast (*Q*-test) to compare young and older adults' effect sizes of the sleep-based memory consolidation.

Second, to examine the age-related alterations on the sleep-based memory consolidation in specific types of memory, we calculated the effect sizes for declarative memory and procedural memory separately for each age group. Again, we computed *Q*-test to compare the age differences between the effect sizes on declarative and procedural memory separately.

Third, if there is significant difference on the sleep-based memory consolidation between young and older adults, we further explore the origination of this difference by testing the age-related differences separately for the sleep and wake condition. For each condition, we calculated the effect size by subtracting the difference in memory performance between the pre-test and post-test in older adults from that in young adults. The direction of the effect size was defined as positive if young adults performed better than older adults. We again used the *Q*-test to evaluate whether the age difference was significant between the sleep and wake conditions.

Fourth, we coded a number of factors that might associate with the sleep-based memory consolidation and used them for our moderator analysis. Significant sleep beneficiations on memory are observed, and some sleep parameters reported in the studies, such as total sleep time, sleep efficiency, sleep onset latency and wake after sleep onset time may be associated with the sleep-based memory consolidation (Aly and Moscovitch, 2010; Cellini, 2016; Peters et al., 2008). We also examined the moderating effect of sex (male vs. female) and experimental design (i.e., between-subjects design vs. within-subjects design) on the sleep-based memory consolidation.

3. Results

3.1. Search results

The initial literature search identified 6883 studies. After study selection based on the inclusion and exclusion criteria, 15 articles examining age-related changes in the sleep-based memory consolidation were included in the present meta-analysis. Some studies investigated both declarative memory and procedural memory. Therefore, the 15 studies contained 22 comparisons, for a total of 622 older adults and 636 young adults. The results of initial reference search and study exclusions are shown in Fig. 2. Table 2 shows a summary of the studies and task information.

3.2. The age-related differences on sleep-based memory consolidation

Our results showed that sleep, compared with an equivalent wake interval, promoted memory performance for young adults (d =0.725, p < 0.001) but not for older adults (d =0.196, p=0.155; Table 3). Fig. 3 presents the forest plots with the respective effect sizes (d) and CI for each study illustrating young and older adults' sleep-based memory consolidation across memory types. The synthesized effect sizes for young and older adults were provided under a random-effects model (Fig. 3, blue diamond). Further, *Q*-test analysis showed that age difference was significant, with young adults having greater effect size than older adults (Q =6.833, p < 0.01), indicating that young adults benefited more from sleep for their memory consolidation than older adults. The homogeneity statistic indicated that both young and older

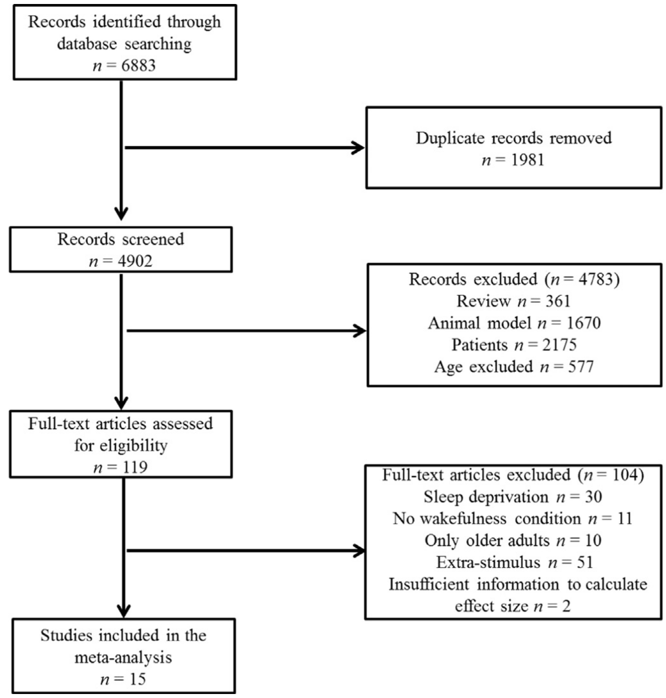

Fig. 2. Flow chart of the study selection process.

adults showed significant heterogeneity among the comparisons, suggesting significant variances in the effect sizes across different comparisons. Egger's test indicated that publication bias was not significant in older adults (t=0.167, p=0.869), but it was significant in young adults (t=3.559, p < 0.001; Table 3).

3.3. Age differences of sleep-based memory consolidation in specific memory types

For declarative memory consolidation, as shown in Table 3, the effect size was significant for young adults (d =1.140, p < 0.001) but not for older adults (d =0.252, p=0.188; Fig. 4A). The *Q*-test results demonstrated that the benefits of sleep on declarative memory, compared with an equivalent interval of wakefulness, were significantly less in older adults than in young adults (Q =6.371, p < 0.010). In turn, concerning procedural memory consolidation, young adults benefited from sleep with a moderate effect size (d =0.470, p < 0.001), whereas the older adults did not receive significant benefits from sleep compared with wake interval (d =0.273, p=0.159; Fig. 4B). However, further *Q*-test analysis showed that the difference in procedural memory consolidation between the two age groups was not significant (Q =0.990, p=0.320). For both declarative memory and procedural memory in young and older adults, homogeneity statistic demonstrated significant variances in the effect sizes, and publication bias was found in declarative memory for young adults (t=5.527, p < 0.010; Table 3).

3.4. The age-related differences in the sleep and wake condition

The foregoing analyses showed that sleep plays a vital role in promoting memory consolidation in young adults, but much less so in older adults. However, it is unclear whether this age difference came from the sleep condition or the wake condition. To further explore the origination of age-related differences in the sleep-based memory consolidation effect, we assessed the age effect in the sleep and wake condition separately. Our results showed that young adults received more benefits than older adults in both the sleep condition (d =0.910, p < 0.001) and the wake condition (d =0.440, p < 0.001; Fig. 5). In the further *Q*-test analysis, we compared the age effects in the sleep

Table 2
Studies included in the meta-analysis.

Study	Age (*SD*)		[a]Sleep efficiency (%)/ [b]Total sleep time (h)		[c]SOL (min)/[d]WASO (min)		Sample size		Procedural task	Declarative task
	Young	Old	Young	Old	Young	Old	Young	Old		
Aly and Moscovitch 2010	19–29	69–80	–	–	–	–	10	12	–	Question List/logical Memory
Baran et al. (2016)	23.2(2.6)	67(3.4)	7.1(1.0)[b]	7.9(1.1)[b]	16.7(11.1)[c] 62.8(36.8)[d]	12.7(5.6)[c] 45.1(31.7)[d]	13	13	–	Association Memory
Bottary et al. (2016)	20.5 (1.45)	67.7(5.9)	92.44(7.98)[a] 6.64(1.32)[b]	92.58(4.40)[a] 7.13(0.56)[b]	10.21(7.25)[c] 19.65(26.64)[d]	9.77(7.97)[c] 24.97 (19.38)[d]	34	39	sequence learning	–
Cherdieu et al., 2014	22.1(1.7)	68.9(5.3)	85.4(2.8)[a] 7.8(0.3)[b]	73.2(19.9)[a] 6.8(0.3)[b]	41.6(12.1)[c] 72.7(12.7)[d]	57.3(11.5)[c] 106.8(2.5)[d]	20	20	–	Association Memory
Fogel et al. (2014)	24(3.8)	62.2(5.0)	76.1(3.9)[a]	49.3(7.8)[a]	11.9(1.9)[c] 10.9(2.7)[d]	18.4(5.3)[c] 31.1(6.8)[d]	30	30	Sequence learning task	–
Gudberg et al., 2015	24.5(0.9)	66.7(3.0)	81.4(1.0)[a] 6.2(0.1)[b]	84.2(1.7)[a] 6.1(0.1)[b]	17(0.04)[c]	11(0.03)[c]	26	21	(Adapted) Sequence learning task	–
Jones et al. (2016, Exp. 1)	20.39 (2.19)	64.08 (8.15)	92.84(1.24)[a] 7.0(0.22)[b]	93.51(1.01)[a] 7.28 (0.14)[b]	–	–	81	51	–	Emotional Picture Recognition
Jones et al. (2016, Exp. 2)	20.26 (1.18)	65.26 (8.16)	94.67(1.24)[a] 6.79(0.30)[b]	91.60(2.04)[a] 6.67 (0.28)[b]	–	–	89	51	–	Emotional Picture Recognition
Mander et al. (2013)	20.4(2.1)	72.1(6.6)	96.3(2.2)[a] 7.8(0.6)[b]	82.6(13.2)[a] 6.9(1.1)[b]	14.8(9.1)[c]	46.2(56.1)[c]	18	15	–	Association Memory
Mantua et al. (2015)	21.2(2.8)	63.9(7.7)	94.2(7.0)[a] 7.0(1.0)[b]	90.29(7.3)[a] 6.7(1.0)[b]	9.8(12.1)[c] 16.1(22.8)[d]	7.7(7.9)[c] 36.0(39.1)[d]	62	61	Mirror Tracing Task	–
Nemeth et al. (2010)	21(1.2)	69.8(7.3)	–	–	–	–	25	24	Sequence learning task	–
Pace-Schott and Spencer (2013)	20.1(0.4)	62.0(2.5)	7.7(0.5)[b]	7.4(0.7)[b]	–	–	31	25	Sequence learning task	–
Sonni and Spencer (2015)	21.4(2.7)	63.6(4.8)	88.2(15.5)a 6.8(1.1)[b]	87.2(8.7)a 6.6(0.9)[b]	13.3(16)[c] 17.6(19.4)[d]	11.3(10.6)[c] 45.7(33.2)[d]	111	75	–	Association Memory
Spencer et al. (2007)	20.8(2.1)	59.0 (11.1)	–	–	–	–	38	32	Sequence learning task	–
Vien et al. (2016)	24.5(4.0)	62.8(4.0)	76.05[a] 1.2[b]	49.31[a] 0.82[b]	0.20[c]	0.31[c]	28	29	Sequence learning task	–
Wilson et al. (2012)	20–34	51–70	6.9(1.0)[b]	6.6(1.3)[b]	–	–	24	31	Sequence learning task	Association Memory

Note:
[a] Sleep efficiency
[b] Total sleep time.
[c] SOL = Sleep onset latency;
[d] WASO = Wake after sleep onset time

condition and wake condition, and found a significant difference (Q =7.299, $p < 0.010$) with larger age differences in the sleep condition than in the wake condition.

3.5. Moderator variables analysis

As shown in Table 4, the influences of potential moderators were

Table 3
Characteristics and main findings of the studies included in the meta-analysis of young and older adults.

Memory system	N of comparisons		Total *N* of subjects		Weighted ES (*d*)		95% CI		Test of homogeneity (*Q*)		Egger's test (*t*)	
	Young	Older	Young	Older	Young	Older	Young	Older	Young	Older	Young	older
Across memory systems	22	22	640	529	0.725	0.196	0.445–1.005	−0.071–0.469	94.565 [***]	95.007[***]	3.559[**]	0.167
Declarative memory	10	10	366	268	1.140	0.252	0.585–1.695	−0.107–0.653	69.950[***]	34.027[***]	5.527[**]	1.267
Procedural memory	12	12	298	292	0.470	0.273	−0.165–0.640	−0.123–0.627	25.548[*]	54.119[***]	0.305	0.886

Note: [*]$p < 0.05$, [***]$p < 0.01$, [***]$p < 0.001$.

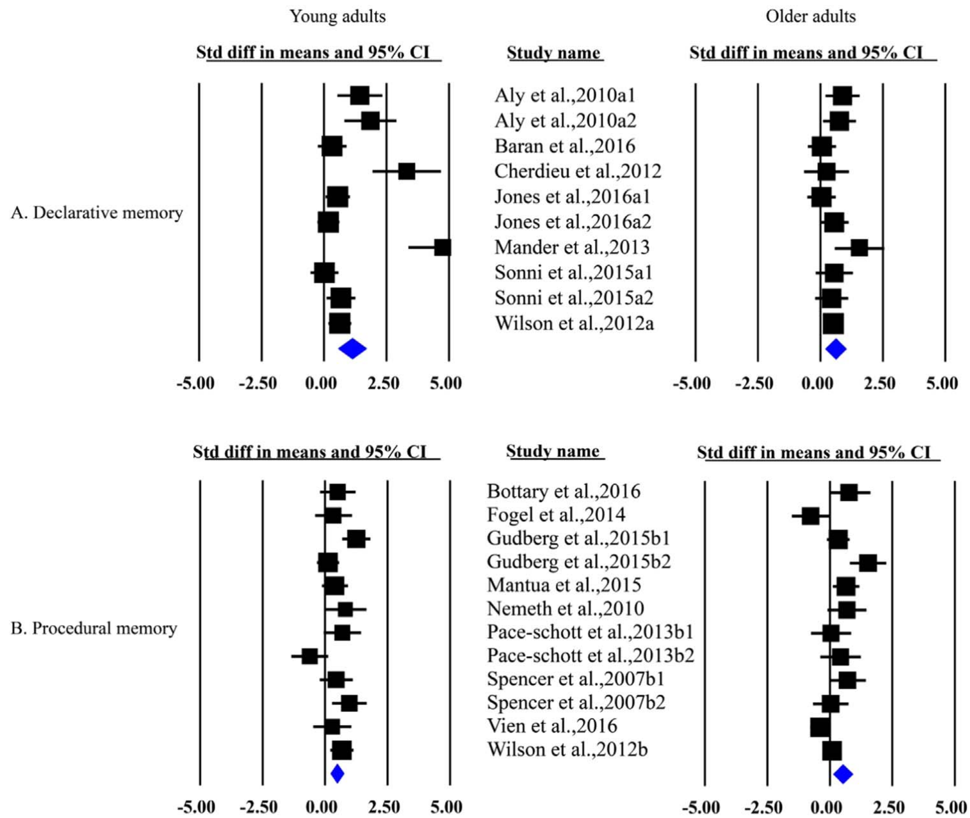

Fig. 3. Sleep-based consolidation effect in young and older adults. Forest plots show the differences between sleep and wake conditions in young (on the left) and older adults (on the right) respectively. The serial number of a and b indicated different memory systems in one study, the number of 1 and 2 indicated different tasks within each memory system. The positions of the squares on the *x*-axis indicate the effect size for each study; the bars indicate the 95% confidence intervals of the effect sizes; the blue diamond indicates the summary effect size for young and older adults respectively.

assessed for the sleep-based memory consolidation effect in young and older adults separately. For each moderator variable, weighted mean effect size (ES) plus 95% CI was calculated. For young adults, meta-regression analysis indicated that total sleep time was positively associated with the effect size of their sleep-base memory consolidation (Q =9.891, $p < 0.010$), while sleep onset latency was negatively associated with it (Q =13.083, $p < 0.010$). For older adults, sleep efficiency positively correlated with the effect size of sleep-base memory consolidation (Q =14.860, $p < 0.010$), while sleep onset latency was negatively correlated with it (Q =11.229, $p < 0.010$).

4. Discussion

In the present study, we applied a meta-analysis to quantify age-related differences in sleep-based memory consolidation. We considered memory types involving both declarative and procedural memory. Overall, young adults benefited from sleep on memory consolidation, whereas older adults showed no sleep-related gains in memory retention. Specifically, older adults had impaired sleep-based declarative memory consolidation but relatively reserved procedural memory consolidation when compared with their younger counterparts. Moreover, these age-related differences on the sleep-based memory consolidation are mainly derived from the sleep condition rather than the wake condition.

4.1. The age-related decline in the sleep-based memory consolidation

Previous studies have confirmed the beneficial effect of sleep on memory consolidation in healthy young adults: compared with a wake interval of equal length, a period of post-learning sleep enhances retention of memory (Born and Wilhelm, 2012; Diekelmann and Born, 2010; Jenkins and Dallenbach, 1924; Lahl et al., 2008; Plihal and Born, 1997). Our meta-analysis findings suggested that this sleep-based memory consolidation typically observed in young adults might be weakened or otherwise diminished in healthy older adults. Combined with findings from previous studies, we considered two perspectives that might account for older adults' declining of sleep-based memory consolidation. First, the functional changes of sleep and memory may independently demonstrate the decline of sleep-based memory consolidation in older adults (Harand et al., 2012; Hornung et al., 2005). For example, age-related changes in sleep quantity and quality may affect sleep-related memory processing in older adults, leading to a weakened sleep-based memory consolidation effect. If so, effective sleep intervention might improve memory consolidation in older adults. In line with this, age-related deteriorations in general memory function may affect the encoding processes in the first place, which may affect the consolidation processes subsequently in older adults (Hornung et al., 2005). Second, the smaller effect size in older adults' sleep-based memory consolidation may be due to "functional weakening", the decreasing resilience in the sleep-memory link as people age (Pace-Schott and Spencer, 2011; Scullin, 2013; Scullin and Bliwise, 2015). It has been hypothesized that memory consolidation relies on the "hippocampal-neocortical dialogue" that facilitates the transfer of information from short-term representations in the hippocampus to long-term storage in the neocortex. With age, some memory related brain areas such as the prefrontal cortex and hippocampus are undergoing structural and functional alterations (Kalpouzos et al., 2009; Mander et al., 2013; Mueller and Weiner, 2009). Moreover, some neurochemical mechanisms, such as cortisol and acetylcholine also exhibit hypofunction (Buckley and Schatzberg, 2005; Schliebs and Arendt, 2006). All these neuronal changes with age may interact with each other and block the transfer of information from the hippocampus

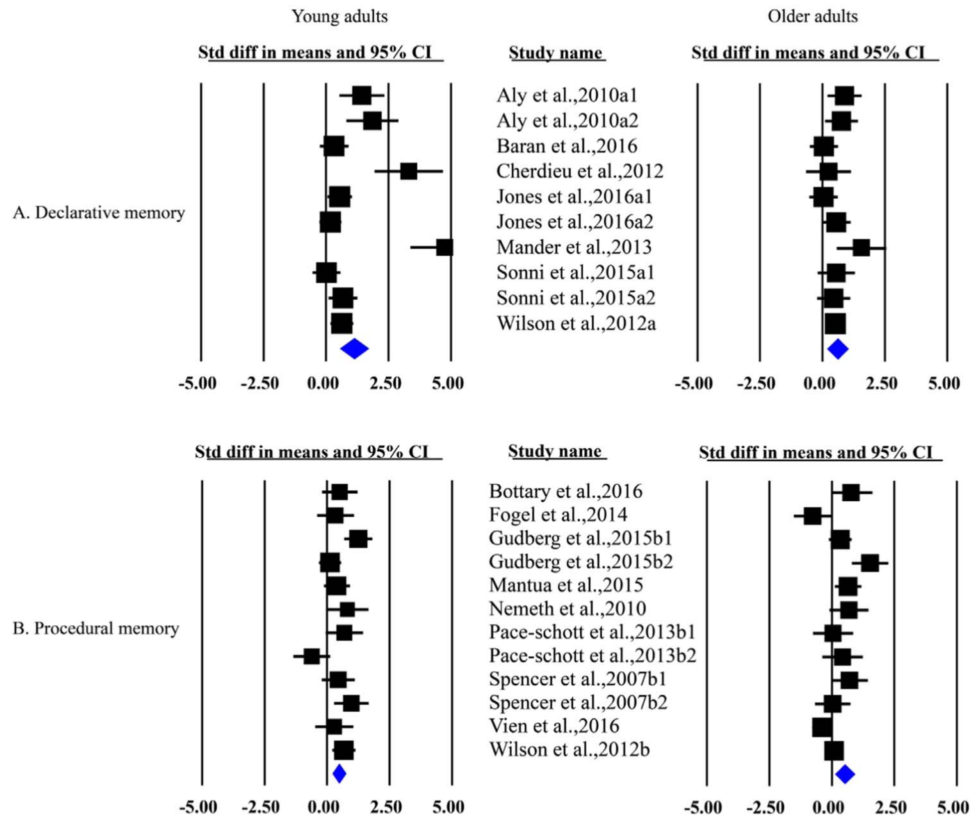

Fig. 4. Sleep-based consolidation effect of A) declarative memory and B) procedural memory in young and older adults. The serial number of a and b indicated different memory systems in one study, the number of 1 and 2 indicated different tasks within each memory system. The positions of the squares on the *x*-axis indicate the sleep-based memory consolidation effect size for each study; the bars indicate the 95% confidence intervals of the effect sizes; the blue diamond indicates the summary effect size of sleep-based memory consolidation for young and older adults respectively.

to the neocortex, thus impairing the sleep-memory link. These may also imply that even with enough sleep memories will not be consolidated as efficiently during sleep in older adults (Harand et al., 2012; Kronholm, 2012; Pace-Schott and Spencer, 2011; Scullin, 2013; Scullin and Bliwise, 2015).

Recently, Scullin and Bliwise (2015) reviewed research from seven distinct domains, ranging from large-scale correlational studies assessed by self-report to experimental studies that manipulated sleep

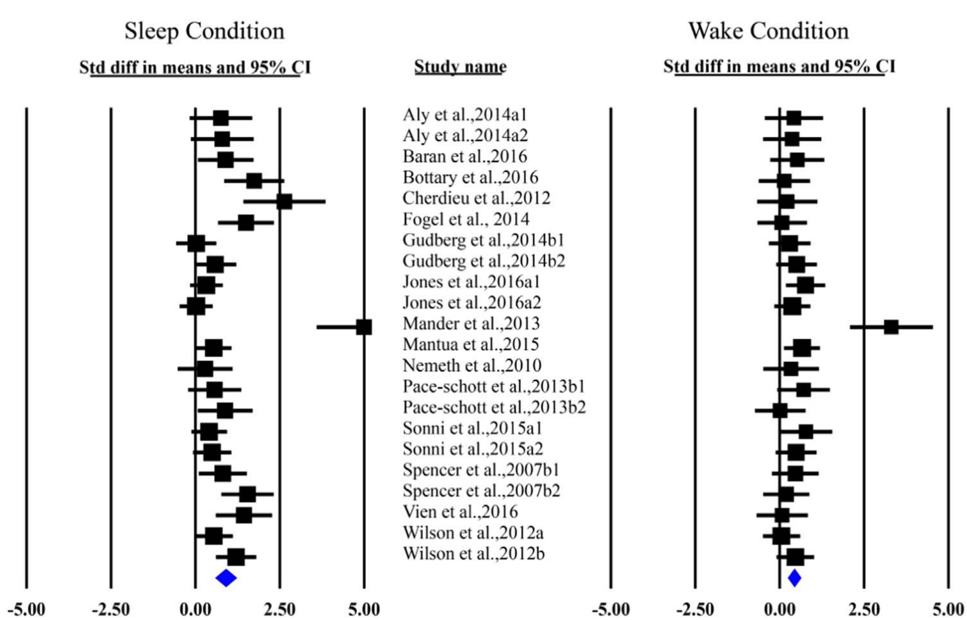

Fig. 5. The age-related differences in the sleep and wake condition. Forest plot for studies analyzed the age effect within the sleep and wake condition respectively. The age effect of performance changes with sleep interval was shown on the left, while the age effect of performance changes with wake interval was shown on the right. The serial number of a and b indicated different memory systems in one study, the number of 1 and 2 indicated different tasks within each memory system. The positions of the squares on the *x*-axis indicate the effect size for each study; the bars indicate the 95% confidence intervals of the effect sizes; the blue diamond indicates the summary effect size of sleep-based memory consolidation for young and older adults respectively.

Table 4
Analyses of potential moderators for sleep-based memory consolidation in the two age groups.

Moderator variable	ComparisonsN	Mean ES	95% CI	Q	p
Sleep efficiency$_{young}$ (%)	12	0.801	0.390–1.212	0.052	0.819
Sleep efficiency$_{older}$ (%)	12	0.065	−0.401–0.531	14.860**	0.001
Total sleep time$_{young}$ (h)	13	0.786	0.412–1.159	9.891**	0.010
Total sleep time$_{older}$ (h)	13	0.126	−0.300–0.552	1.545	0.214
Sleep onset latency$_{young}$ (min)	11	0.870	0.404–1.335	13.083**	0.001
Sleep onset latency$_{older}$ (min)	11	0.018	−0.485–0.521	11.229**	0.001
Wake after sleep onset$_{young}$ (min)	7	1.385	0.385–2.065	0.806	0.369
Wake after sleep onset$_{older}$ (min)	7	0.145	−0.324–0.614	0.148	0.701
% of male participant$_{young}$	16	0.732	0.418–1.046	0.668	0.414
% of male participant$_{older}$	16	−0.078	−0.380–0.223	1.614	0.204
Experiment design$^{a}_{young}$	22	0.723	0.454–0.992	0.025	0.875
Experiment design$_{older}$	22	0.063	−0.222–0.348	2.198	0.138

Note: ES = Effect Size; $^{**}p < 0.01$, $^{***}p < 0.001$

duration and quality. They suggested that the inter- and intravariability in sleep often do not relate to cognitive function, and solely improving sleep may not reverse cognitive impairments in older adults. Besides the “functional weakening” explanation, they also proposed other four possible perspectives to account for the null effects in older adults, as sleep does not related to cognitive functions, even in young adults; the findings might be masked by the limitation of measurement; reduced need for sleep and compensation theory of neurocognitive aging.

4.2. Declarative memory consolidation vs. procedural memory consolidation

Our results indicated different patterns of age-related alterations in sleep-based memory consolidation of different types of memory. Specifically, older adults showed functional decline in sleep-based declarative memory consolidation, but relatively spared in procedural memory consolidation.

In young adults, declarative memory consolidation has been linked to SWS or sleep spindles (Diekelmann and Born, 2010; Fogel and Smith, 2011; Plihal and Born, 1997). In older adults, there are dramatic changes in SWS and the associated slow oscillations (Ohayon et al., 2004), which may account for their declining consolidation of declarative memory during sleep. Moreover, along with aging processes, declarative memory-related regions such as the prefrontal cortex undergo functional changes (Kalpouzos et al., 2009; Pini et al., 2016). For example, Mander et al. (2013) showed that age-related prefrontal cortex atrophy was associated with reduced slow wave activity (SWA) in older adults, which mediated the impairment of declarative memory retention. Moreover, the declining retention effect was further associated with persistent hippocampal activation and reduced functional connectivity between the hippocampus and the prefrontal cortex, potentially representing an impoverished hippocampal-neocortical memory transformation. Recently, a functional-dissociation interpretation proposed by Scullin (2013) suggested that the link between SWS and declarative memory that is typically observed in young adults might be weakened or otherwise functionally changed in healthy older adults.

For the procedural memory consolidation, no significant age difference was found in the current meta-analysis. On the one hand, procedural memory consolidation mainly engages the motor-related brain regions, such as cerebellum, putamen, and parietal cortex (Barnes et al., 2005; Doyon et al., 2003; Fogel et al., 2014; Rasch et al., 2007), which may be relatively intact in older adults. On the other hand, procedural memory consolidation may appear to be spared due to compensation. In a pursuit rotor procedural memory task, researchers found that there was no group difference when a relative measure of improvement (percent increase across sessions) was used (Peters et al., 2008). More interestingly, they found an increase in SWS after learning in the older adults but not in young adults. They suggested that the increase in SWS in older adults could have been some kind of compensatory responses by the brain following task acquisition.

4.3. Moderators for the sleep-based memory consolidation in young and older adults

The moderator variable analyses highlighted the importance of sleep onset latency on the sleep-based memory consolidation for both age groups – participants with longer sleep onset latency had smaller effect sizes of sleep-based memory consolidation. Since the longer the sleep onset latency, the less percentage of SWS and REM there would be. This could affect the dialogue between memory-related brain areas and may impair the memory consolidation processing (Diekelmann et al., 2009).

Moreover, the meta-regression analyses also showed that older adults with less sleep efficiency had smaller effect size of the sleep-based memory consolidation. Sleep efficiency reflects the quality of sleep and is important for memory consolidation processes (Moraes et al., 2014). Older adults typically show reduced sleep efficiency, as they tend to have longer sleep onset latency and more sleep fragmentation at night (Crowley, 2011; Hornung et al., 2005; Pace-Schott and Spencer, 2011). As we known, sleep fragmentation may induce difficulties maintaining continuous sleep during the night, and thus influence the transformation between NREM and REM sleep, disrupting memory consolidation processes (Carskadon et al., 1983). Indeed, Cellini (2016) recently suggested that sleep fragmentation could induce sleep-related impairment in the consolidation of declarative and procedural information. Sleep fragmentation is also associated with the onset of Alzheimer's Disease and the rate of cognitive decline (Lim et al., 2013). The present meta-regression supported the aforementioned findings by showing a positive correlation between sleep quality and memory consolidation. However, whether such changes in sleep physiology affect older adults’ memory consolidation remains to be discerned. Future work could directly test the role of sleep architecture and neuroendocrine deficits in age-related memory consolidation by using behavioral performance indices in neurobiological, cardiovascular, or endocrine moderator analyses (Scullin and Bliwise, 2015).

4.4. Limitations

This analysis contains some limitations due to the current state of the field. First, only a small number of studies on the sleep-based memory consolidation and aging fulfilled our selection criteria. This resulted in a relatively small sample size in the current analysis and may provide an incomplete view of the results. Second, although every effort was made in this analysis to attribute studies to testing the sleep benefiting effect on declarative or procedural memory, the diversity of tasks within each type of memory may have affected the validity of the conclusions. Third, although we tried to control as many factors that may influence sleep-based memory consolidation as possible in our analysis, there are still some that we could not take into account, as the data were not available in the original articles, such as the percentage of different sleep stages (e.g., SWS and REM) that may associate with the sleep-based memory consolidation to a great degree. Finally, publication bias was found in young adults, which may influence the reliability of the results.

5. Conclusion

In General, older adults have a decline in sleep-based memory consolidation relative to young adults across memory types. Moreover, this age-related degradation in the sleep-based beneficial effect is mainly manifested in declarative memory relative to procedural memory. We discussed possible neural substrates of these age-related differences. However, no neuroimaging studies have directly examined the brain mechanisms underlying the alterations of sleep-based memory consolidation in older adults. 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.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (31300856 to J.Y. and 31571111 to X.L.), the Doctoral Fund of the Ministry of Education of China (20130182120013 to J.Y.), the Fundamental Research Funds for the Central Universities (SWU1509421 to J.Y.) and the Key Laboratory of Mental Health, Institute of Psychology, Chinese Academy of Sciences (KLMH2015G05 to J.Y).

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