The Prospective Sleeping Brain: Age-Related Differences in Episodic Future Thinking and Frontal Sleep Spindles

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Abstract

■ Sleep spindles are a physiological marker of off-line memory consolidation. In young adults, sleep spindles are preferentially responsive to encoded information that is tagged as having future relevance. Older adults, on the other hand, show reduced capacity for future simulation and alterations in sleep physiology. Healthy young adults (n = 38) and older adults (n = 28) completed an adaptation night, followed by two in-laboratory polysomnography nights, in which they mentally simulated future events or remembered past events, recorded via written descriptions. We quantified the degree of future/past thinking using linguistic analysis of time orientation. In young adults, greater future thinking was linked to greater spindle density, even when controlling for gender, age, and word count (r_p = .370, p = .028). The opposite was true for older adults, such that greater future thinking was associated with reduced spindle density (r_p = −.431, p = .031). These patterns were selective to future thinking (not observed for past thinking). The collective findings implicate an impaired interaction between future relevance tagging and sleep physiology as a mechanism by which aging compromises sleep-dependent cognitive processing. ■

INTRODUCTION

The classic view of sleep is that it functions to restore the body following daytime use. Indeed, sleep restores glycogen levels, clears metabolites, and downregulates synaptic weights. When sleep is lost, it must be recovered, otherwise daily functioning becomes sluggish, the immune system is more easily compromised, and risk for diseases/disorders increases (Luyster, Strollo, Zee, & Walsh, 2012). Slow wave activity (delta power) is typically used to index sleep homeostasis or, in other words, the degree to which sleep is needed to restore the brain and body in response to the previous day (Borbély, 1982).

Though few scholars debate that sleep serves restorative functions, the discovery that memories are reactivated and consolidated during sleep challenges the notion that sleep's role is simply to homeostatically regulate the brain (Rasch & Born, 2013). Memory functioning, after all, is a future-oriented ability. It serves little functional value to veridically store all experiences from the past; instead, memory systems evolved to aid survival in the present and guide future behaviors (Schacter et al., 2012).

One model of memory consolidation is that encoded information must be tagged as future relevant to undergo consolidation during sleep (Stickgold & Walker, 2013). Broadly speaking, such tagging may occur based on expected future rewards, emotionality, and saliency of encoded experiences. Selective or preferential consolidation has been reported for memories for future actions (Scullin et al., 2019; Barner, Seibold, Born, & Diekelmann, 2017), for highly rewarded memories (Michon, Sun, Kim, Ciliberti, & Kloosterman, 2019; Oudiette, Antony, Creery, & Paller, 2013; Fischer, & Born, 2009), for "remember" but not "forget" items in directed forgetting lists (Scullin, Fairley, Decker, & Bliwise, 2017; Saletin, Goldstein, & Walker, 2011), and when individuals are explicitly instructed to expect a later retrieval test (Bennion, Payne, & Kensinger, 2016; Van Dongen, Thielen, Takashima, Barth, & Fernández, 2012; Wilhelm et al., 2011; for alternative findings, see Cordi & Rasch, 2021; Reverberi, Kohn, & Fernández, 2020; Wamsley, Hamilton, Graveline, Manceor, & Parr, 2016). A sleep-based hippocampal–neocortical dialogue is hypothesized to underlie consolidation of future-relevant memories, with this dialogue being indexed in humans using scalp EEG measures of spindle density (Studte, Bridger, & Mecklinger, 2017; Saletin et al., 2011), slow wave activity (Oudiette et al., 2013), or both (Wilhelm et al., 2011).

An important but unresolved question is whether and how aging compromises sleep-dependent memory consolidation (Spencer, Gouw, & Ivry, 2007). Memory consolidation is presumed to be a building block of overall cognitive functioning, with cognitive functioning known to decline progressively across the adult life span to the point that independent living becomes disrupted (e.g., early stages of Alzheimer disease and related dementias). The preponderance of evidence points to memory consolidation being reduced or absent even in healthy older adults (Leong, Lo, & Chee, 2021; Jones, Mackay, Mantua, Schultz, & Spencer, 2018; Gui et al., 2017). However, researchers are still

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determining the psychological and neurobiological mechanisms by which memory consolidation declines with aging (Scullin & Gao, 2018; Mander, Winer, & Walker, 2017). For example, memory consolidation may decline with aging because of changes in the neuroanatomy of cognitive systems, alterations in spindle and slow wave physiology, changes in encoding quality, or some combination of these cognitive–sleep–neuroanatomical mechanisms (Muehlroth, Rasch, & Werkle-Bergner, 2020; see also Huan, Liu, Lei, & Yu, 2020; Alger, Kensinger, & Payne, 2018). Building on this "combination" view, we hypothesized that there are changes in the aging brain's ability to tag encoded information as future relevant in a manner that effectively triggers sleep physiological responses. We investigated this possibility by examining sleep physiology markers in response to a hippocampus-dependent intensive future-thinking task (Addis, Wong, & Schacter, 2007).

METHODS

Participants

Sixty-six healthy participants spent three nights in the sleep laboratory. The sample included 38 young adults (ages 18–29 years, M_{age} = 20.37 ± 1.67 years, 57.9% women, 57.9% white) and 28 older adults (ages 50–84 years, M_{age} = 65.50 ± 9.07 years, 53.6% women, 82.1% white). Participants were recruited from the central Texas area using outreach programs, fliers, and local news advertisements for a larger study of sleep, cognition, and aging (Scullin et al., 2019). Inclusion criteria were being 18 years or older and scoring 24 or higher on the Mini-Mental Status Examination (M_{Young} = 28.63 ± 1.26, M_{Older} = 27.96 ± 1.79; Folstein, Folstein, & McHugh, 1975). Exclusion criteria were having a history of psychiatric or neurological disorders, insomnia, or narcolepsy; taking sleep-altering medications; showing an apnea–hypopnea index of ≥30 on the adaptation night; or not completing all three laboratory nights. Participants gave informed consent, and the study was reviewed and approved by the Baylor University institutional review board.

Sleep Measurement

Grass Comet XL Plus systems were used for overnight polysomnography. Recordings were taken in a sound-dampened sleep laboratory at Baylor University. The montage included EEG, recorded at 200 samples per second, at positions Fp1, Fp2, F3, F4, Fz, C3, C4, Cz, P3, P4, Pz, O1, and O2, using contralateral mastoids as reference points. EOG (left and right), mentalis EMG, and measures of breathing (i.e., nasal pressure, chest and abdomen movements, and finger pulse oximetry) were also included. A certified polysomnography technician scored sleep stages in 30-sec epochs according to American Academy of Sleep Medicine guidelines (Iber, Ancoli-Israel, Chesson, & Quan, 2007).

Quantitative EEG Analysis

We utilized MATLAB (2019a; Mathworks, Inc.) to conduct spectral analysis of the EEG. Trained research personnel excluded epochs containing movement or other artifacts (averaging 1.82% of all epochs). Following this, data were re-referenced to the common average, band-pass filtered utilizing a high-pass cutoff of 0.3 Hz and a low-pass cutoff of 35 Hz, and down-sampled to the next power of two (128 Hz), to allow for even spacing of points in subsequent spectral analysis (Cooley & Tukey, 1965). For each stage of sleep (N1, N2, N3, REM, and NREM), power was computed using Welch's method, using a symmetric 4-sec Hanning window with 50% overlap, at a resolution of 0.25 Hz, generating a spectral power density (μV^2/Hz) at all scalp channels. Next, data were corrected for aperiodic noise components using the fitting oscillations and one-over f method (Donoghue et al., 2020), which outputs log-transformed values suitable for parametric analysis. Finally, mean spectral power density was generated for typical frequency bands: 0.5–1 Hz (slow oscillations), 1–4 Hz (delta), 4–8 Hz (theta), 8–12 Hz (alpha), 12–16 Hz (sigma), and 16–32 Hz (beta). Because slow wave activity, particularly in the frontal lobe, is known to change with age (Muehlroth & Werkle-Bergner, 2020; Mander et al., 2017), we were primarily interested in slow wave activity, operationalized as slow oscillation and delta power averaged across frontal sites (Fp1, Fp2, F3, F4, and Fz) during NREM.

In a separate analysis pipeline, automated spindle detection was conducted based on the algorithm described by Wamsley et al. (2012), which performs time–frequency analysis of the EEG using Morlet wavelets. Average-referenced data were resampled to 100 Hz, and spindle detection was conducted separately for each channel during artifact-free epochs via identifying amplitude increases (>4.5 times of mean signal) occurring in the canonical spindle frequency band (10–16 Hz) and lasting between 0.3 and 3 sec. This procedure has been validated relative to trained manual scoring and appears to outperform other automated spindle detection tools (Warby et al., 2014). Spindle density was the number of spindles per minute averaged across frontal sites during NREM.

Procedure

After completing an adaptation night, participants returned to the laboratory for two experimental nights (89.5% within 2 days, 100% within 1 week). On arrival, participants completed questionnaires, had electrodes applied, and completed 30 min of cognitive and memory tasks (data reported in Scullin et al., 2019). Afterward, participants completed an episodic future-thinking task or a past-thinking task using the Modified Future Crovitz Test (MFCT; Crovitz & Schiffman, 1974). In the MFCT, participants are shown a common noun (e.g., apple) and asked to generate and type in detail either a related past memory

or simulate a novel future event. Future simulation in the MFCT is a hippocampus-dependent ability (e.g., Addis et al., 2007). On one night, participants completed only future-thinking simulations, and on the other night, participants completed only past thinking (night order counterbalanced). There were 10 trials each night, with different lists of nouns each night (order counterbalanced). On each trial, participants viewed the cue word for 3.5 sec and then typed their response for 60 sec. Participants were in bed with lights out by 22:30 and with lights on at 07:30 the next morning, giving approximately 9-hr time in bed.

Linguistics Analysis

To index the intensity of future/past thinking, we subjected participants' typed responses on the MFCT to computerized text analysis using Linguistic Inquiry and Word Count Version 1.3.1 (LIWC, 2015; Pennebaker, Booth, Boyd, & Francis, 2015). Using the Java programming language, LIWC software compares digitized text against a built-in dictionary to produce weighted estimates of cognitive and psychological variables. Before analysis, the data were preprocessed for spelling errors. Although LIWC extracts dozens of linguistic markers, our focus was on extractions of time orientation (future/past tense dominance). All LIWC analyses were adjusted for total word count.

Statistical Analysis

We first compared the age groups on LIWC time orientation, spindle density, and slow wave activity outcomes. Next, we conducted regression analyses to determine whether greater future thinking was associated with sleep physiology in young and older adults. For quantitative EEG analyses, we controlled for sex and chronological age given the known decline in spindle density and slow wave activity in male (relative to female) individuals and with each advancing decade (Fernandez & Lüthi, 2020; Wilckens, Ferrarelli, Walker, & Buysse, 2018). As a control, we repeated the analyses with the degree of past thinking (on past-thinking nights). Primary statistical analyses were conducted in SPSS Version 27, and all tests were two-tailed with alpha set to .05. For spatial visualization of our main effects, we conducted individual-channel follow-up correlation analyses in MATLAB, using a Bonferroni-corrected alpha of .05/# channels ($p < .0038$), with r values Fisher-transformed to z values for ease of interpretation.

RESULTS

To assess the relationship between brain activity in aging and future/past orientation, we conducted a series of 2 (Age) × 2 (Night) ANOVAs on the quantitative EEG measures. Figure 1 illustrates significant age-related decline in frontal delta power density, $F(1, 63) = 39.46$, $p < .001$, $\eta_p^2 = .385$, frontal slow oscillation power density, $F(1, 63) = 28.40$, $p < .001$, $\eta_p^2 = .311$, but not in frontal spindle density, $F(1, 62) = 0.14$, $p = .712$, $\eta_p^2 = .002$. There were no interactions with Night after adjusting for age and sex covariates ($ps > .05$). These patterns confirm previous evidence that the aging brain produces less slow wave activity (Mander et al., 2017) but diverge somewhat from findings of fewer spindles in older individuals (Fernandez & Lüthi, 2020).

In terms of behavioral differences between age groups, we also observed an age-related impairment in episodic future thinking (Figure 2). After adjusting for total word count, the 2 (Age) × 2 (Tense) ANCOVA showed a significant interaction, $F(1, 63) = 10.44$, $p = .002$, $\eta_p^2 = .142$. Young adults showed a greater future index than older adults on the future-thinking night, $F(1, 63) = 7.78$, $p = .007$, $\eta_p^2 = .110$; this age difference in episodic future thinking was observed without significant alterations to past focus scores that night, $F(1, 63) = 3.08$, $p = .084$, $\eta_p^2 = .047$, or alterations to future index scores on the past-thinking night, $F(1, 63) = 0.616$, $p = .435$, $\eta_p^2 = .010$.

On the future-thinking night, there was an age-related divergence in the relationship between LIWC future index scores and subsequent spindle density. Figure 3 illustrates that, after adjusting for covariates, greater future thinking was associated with greater frontal spindle density in the young adults, $r_p(33) = .370$, 95% CI [.042, .626], $p = .028$; interestingly, the opposite pattern emerged in the older adults, $r_p(23) = -.431$, 95% CI [−.706, −.043], $p = .031$. Hierarchical regression analysis on frontal spindle

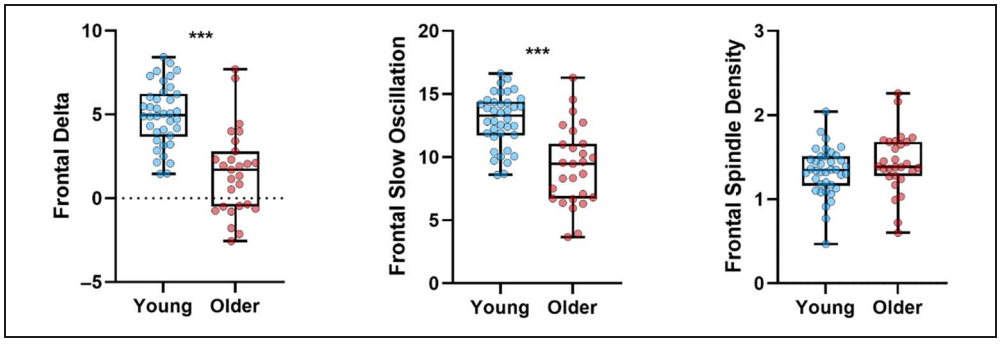

Figure 1. Age-related effects on NREM slow wave activity and spindle density, visualized on the future-thinking night. Older individuals had less average power in both slow oscillation and delta bands but were not different from younger individuals in mean spindle density. Bars represent minimum and maximum values. ***$p < .001$.

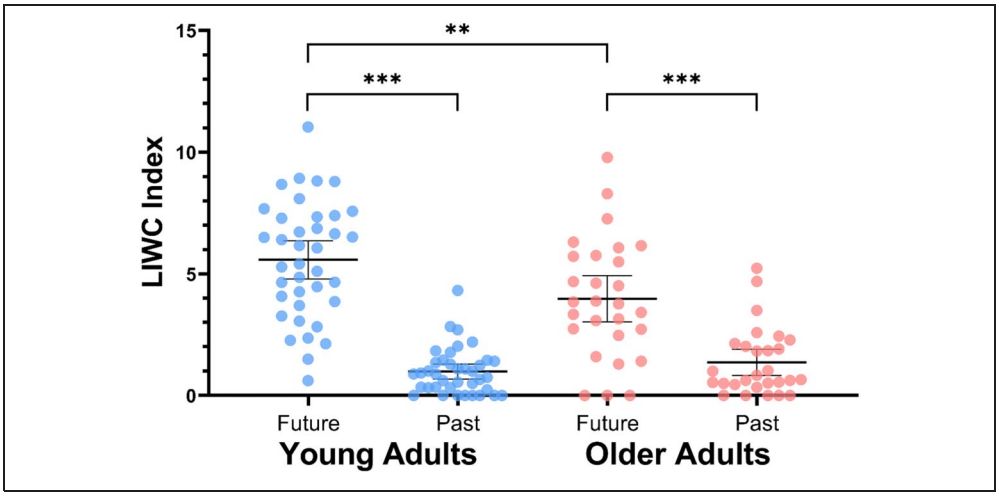

Figure 2. LIWC analyses of time orientation across age groups during the future-thinking night. Error bars represent 95% confidence intervals. $^{**}p < .01$, $^{***}p < .001$.

density provided additional support for this interaction: After entering Age Group, Sex, Future Index, and Word Count in Step 1, $R^2 = .110$, $F(4, 61) = 1.89$, $p = .123$, the Age Group × Future Index interaction in Step 2 explained considerable additional variance in frontal spindle density, $\Delta R^2 = .118$, $F(1, 60) = 9.17$, $p = .004$. To visualize the spatial extent of these effects, we replicated these analyses at the individual-channel level (Figure 4). We found significant relationships at F3/F4 for the young adults and Fp1 in the older adults, in the same directions as the main analysis. We also found similar effects at O1/O2 in the older adults. As expected, none of the relationships between spindle density and past thinking on the past-thinking night were significant.

In sensitivity analyses that excluded participants with Mini-Mental Status Examination scores below 27 ($n = 7$), this age-based dissociation was maintained, with greater future thinking being associated with greater frontal spindle density in young adults, $r_p(30) = .380$, 95% CI [.036, .643], $p = .032$, but lower density in older adults, $r_p(19) = -.487$, 95% CI [−.759, −.070], $p = .025$. The connection between future thinking and sleep physiology was selective to sleep spindles: No significant associations were observed for slow wave activity, which is often used to index sleep pressure/homeostasis (e.g., Borbély, 1982). Furthermore, all correlations were specific to the future condition night: No significant associations were observed for the LIWC future index on the past-thinking night or the LIWC past index in the young or older adults (all ps > .05). Indeed, even when controlling for spindle activity on the past-thinking night, there was still a trend toward associations between greater future thinking and spindle activity on the future-thinking night: younger, $r_p(31) = .342$, 95% CI [−.001, .613], $p = .051$; older, $r_p(21) = -.385$, 95% CI [−.688, .032], $p = .070$. Therefore, the link between future thinking and spindle activity seems night-specific rather than reflecting generalized trait ability of spindle density.

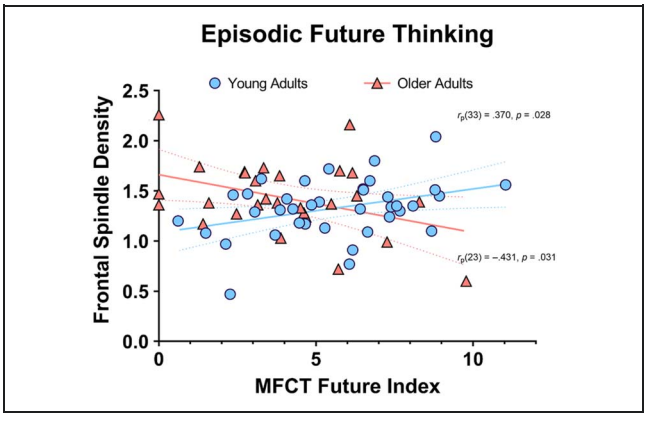

Figure 3. Greater future thinking was associated with higher frontal spindle density in young adults and lower spindle density in older adults (adjusted for age, sex, and word count). The solid lines represent lines of best fit, whereas the dashed lines represent their 95% confidence intervals.

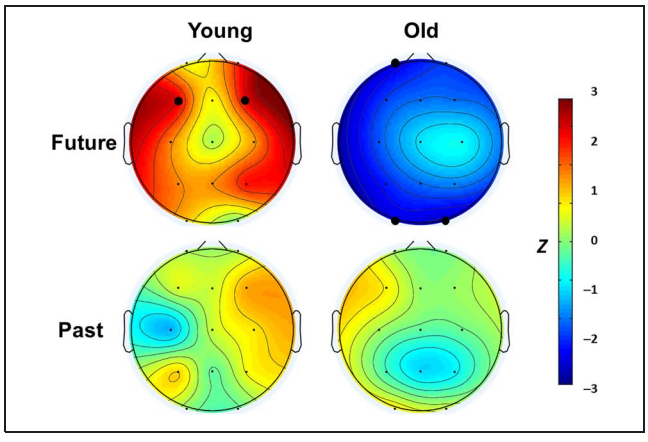

Figure 4. Spatial specificity of future- and past-thinking effects. Individual-channel analyses highlighted where future-thinking relationships with spindle density were greatest for young and older adults; bolded dots indicate corrected $p < .05$. Past-thinking effects were not significantly related to spindle density at any channel in either group.

GENERAL DISCUSSION

The current study demonstrated that spindle density is sensitive to the intensity of recent future simulation. Increased future simulation yielded higher spindling rates in young adults, but lower spindling rates in older adults. These patterns were robust when controlling for sex, cognitive status, word count, and control night spindle density. In this section, we consider these findings relative to the theorized function of sleep spindles and comment on why aging compromises spindle functioning.

Sleep spindles are theorized to represent off-line memory consolidation processes (Fernandez & Lüthi, 2020; Zhang, Yetton, Whitehurst, Naji, & Mednick, 2020). Thalamocortical sleep spindles mediate the coordinated activity of cortical slow oscillations and hippocampal sharp wave ripples (Poe, Walsh, & Bjorness, 2010; Latchoumane, Ngo, Born, & Shin, 2017). In young adults, the coordinated activity of spindles, slow oscillations, and sharp wave ripples helps integrate recently encoded information into long-term memory stores (Staresina et al., 2015). In older adults, this coordinated activity is disrupted (Muehlroth et al., 2019; Helfrich, Mander, Jagust, Knight, & Walker, 2018). Of interest to the current work is evidence that spindling activity is responsive to recent learning experiences (Gais, Mölle, Helms, & Born, 2002), particularly intensive learning of information with future relevance (Studte et al., 2017; Saletin et al., 2011; Wilhelm et al., 2011). Our findings on episodic future thinking are consistent with the hypothesis that spindle activity underlies preferential processing of future-relevant information. In other words, the sleeping brain is prospective—at least in young adults—with its prospective nature partially indexed by spindle activity.

In contrast to the findings in young adults, greater episodic future thinking did not lead to greater spindling in older adults. If future thinking and spindling were simply dissociated in older age, then that would fit well with work that found sleep macro- and microarchitecture to be less commonly linked to cognitive outcomes in older adults than in children and young adults (Scullin & Bliwise, 2015). However, to our surprise, spindling rates in older adults were negatively associated with intensity of recent future thinking. Though there is empirical precedent for this age by spindling dissociation (e.g., Fogel et al., 2017), it remains poorly understood. We see three potential interpretations.

First, there are known encoding deficits in older adults, including deficiencies in simulating the future in detail (Schacter et al., 2013). By this view, only very detailed future simulations may pass a threshold by which spindling rates are increased. Second, there are known alterations to sleep physiology with aging, including increased fragmentation and decreased structural and functional integrity of the brain regions needed to generate and coordinate spindle activity (Mander et al., 2017). By this view, the future-thinking older brain may not be able to trigger spindle bursting because of fragmented sleep, cortical cell loss, or hippocampal cell loss (Fogel et al., 2017). Third, there are changes in time perception with increasing age (socioemotional selectivity theory; Carstensen, 2006). By this view, older adults are more likely to perceive time as finite and therefore are motivated toward thinking about the future in terms of regulating positive feelings and well-being; by contrast, young people perceive time as open-ended and are therefore more likely to think about the future in terms of experiencing novelty and learning new information. Socioemotional selectivity theory, therefore, offers a tantalizing explanation of the current findings: Only specific qualities of future thinking (e.g., learning, experiencing novelty) are sufficient to drive sleep-dependent plasticity processes. Of course, some combination of the above three views may best capture why aging compromises future thinking–sleep physiology interactions.

Muehlroth and Werkle-Bergner (2020) have outlined an excellent list of key methodological concerns in understanding how sleep and aging interact, several of which are worth mentioning here. First, there are many different measures of sleep physiology that might seem similar but show differing effects. For example, we have focused on spindle density in the current work, but there may be additional measures of interest (e.g., SO-spindle coupling). Second, different spindle frequencies (fast vs. slow) can differ in both topography and function and these frequencies can shift over the lifespan, with fast spindles becoming faster and slow spindles becoming slower with increasing age. To minimize the number of statistical tests, in our analyses, we used a single spindle detector and did not differentiate between fast and slow spindles. This approach could potentially cause a decreased number of spindles to be detected in older individuals. However, we saw no significant difference in frontal spindle density between our young and older groups, seeming to indicate that these age-related frequency shifts did not lead to a noticeable loss in the number of detected spindles. Third, the neural generators of sleep measures, such as spindles, are complex and best detailed spatially with MRI and electrode setups that allow and source localization. Such approaches will be advantageous to advancing knowledge of sleep, aging, and future tagging.

In conclusion, though sleep has historically been viewed as a reactive, homeostatic process, it appears now that the sleeping brain is more prospective than previously considered. Restoring glycogen levels, clearing metabolites, and homeostatically regulating synaptic weights are biological necessities, but equally important is preparing the brain for probable future events (Llewellyn & Hobson, 2015). Young adults' sleeping brains do just that. However, with increasing age, there is a disconnect between information tagging (as future relevant) and physiological responses during sleep. Addressing encoding–spindle interactions should illuminate why some adults' cognitive functioning is preserved into older age whereas other older adults' functioning declines.

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Author Contributions

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Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were M(an)/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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