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Greater sleep variance related to decrements in memory performance and event-specific neural similarity: a racially/ethnically diverse lifespan sample

Emily Hokett[a,*], Soroush Mirjalili[b], Audrey Duarte[b,c]

[a] Columbia University, Department of Neurology, New York, NY, USA
[b] University of Texas at Austin, Department of Psychology, Austin, TX, USA
[c] University of Texas at Austin, Department of Neurology, Austin, TX 78712, USA

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ABSTRACT

Successful memory performance depends on overlap between neural representations at encoding and retrieval. With older age, neural similarity, memory performance, and sleep quality decline. Regardless of age, racial/ethnic minorities tend to experience poor sleep, which may contribute to poor memory. Previous studies have not investigated memory performance, neural similarity, sleep quality, and age in diverse participants. Here, we recruited racially/ethnically diverse adults across the lifespan and examined night-to-night sleep quality in relation to memory performance and encoding-retrieval similarity. We employed item-specific, representational similarity analysis (not confounded by effort, word perception, or differences in electroencephalography signal amplitude) to assess neural similarity for intact and recombined paired associates. Greater sleep variance and poorer memory performance were more strongly associated with older age. Interestingly, sleep variance was positively associated with neural similarity for intact pairs. This relationship was stronger with younger age and for racial/ethnic minorities. For recombined pairs, greater sleep variance was associated with reduced neural similarity. Thus, varied sleep may induce greater reliance on familiarity, while consistent sleep may support recollection.

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1. Introduction

Sleep facilitates episodic memory consolidation (for a review, Rasch & Born, 2013). For example, studies that manipulate sleep conditions with either morning versus evening retrieval, sleep deprivation, or intervening naps show that episodic memory (i.e., memory for previously experienced events) is sleep dependent in both young and older adults (Wilson et al., 2012). Similarly, polysomnography studies have demonstrated electroencephalography (EEG) sleep signatures that are indicative of memory consolidation across age (for a review, Mander et al., 2017). However, these studies do not allow for naturalistic sleep assessments measured within the home environment, nor do they typically monitor sleep for more than 1 night.

One of the most common approaches for assessing habitual sleep is actigraphy, which generates multiple parameters, including total sleep time (TST) and sleep efficiency, a measure of sleep continuity, computed by dividing the time spent asleep by the total time in bed. Another measure of sleep continuity is wake after sleep onset (WASO), a sum of minutes spent awake after initial sleep onset. Older adults, as compared to young and middle-aged adults, are more likely to experience chronic sleep disruptions that include reduced TST, decreased sleep efficiency, and exponentially increased WASO (for a review, Ohayon et al., 2004). Older age is associated with greater night-to-night variability in measures of sleep continuity, especially WASO (Shoji et al., 2015). Importantly, these age differences cannot be explained by insomnia, mood disorders, or any clinically significant condition (i.e., Alzheimer's disease; Li et al., 2018).

Poor sleep may contribute to poor memory in older age. Older adults typically perform worse on memory tasks that require recollection-based memory retrieval as compared to familiarity (for a review, Koen & Yonelinas, 2014). For example, associative memory performance declines to a greater extent than does item recognition with older age (for a review, Old & Naveh-Benjamin, 2008). Interestingly, these same types memory tasks are particularly dependent on sleep in young and older adults (for a review, Diekelmann et al., 2009). Age-related differences in

* Corresponding author at: Columbia University, Irving Medical Center 622 W 168th St, New York, NY 10032
E-mail address: ech2175@cumc.columbia.edu (E. Hokett).

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sleep quality have been associated with poorer episodic memory performance using self-report, actigraphy, and polysomnography-measured sleep (Hokett & Duarte, 2019; Mander et al., 2013; Mary et al., 2013). Collectively, these studies demonstrate that young and older adults show associations between sleep quality and episodic memory performance.

In addition to age-related reductions in sleep quality, there are well known racial/ethnic sleep disparities. Previous research has reported lower sleep quantity and quality, detected using self-report, actigraphy, and polysomnography, in racial/ethnic minorities, including non-Hispanic Black and Hispanic adults, than in non-Hispanic White adults (Johnson et al., 2019). In parallel with poorer sleep quality, racial/ethnic minorities sometimes show lower episodic memory performance than other groups (Fyffe et al., 2011). However, racial differences in episodic memory performance are not found when correcting for education quality (e.g., reading level; Fyffe et al., 2011). This suggests that racial differences in episodic memory performance are not inherent to race, and when observed, may be due to differences in education quality or other factors that show inequitable distributions across racial groups.

Neurobiological models of memory posit that successful episodic memory retrieval is dependent upon the reinstatement of encoding-related neural activity and associated operations (Norman & O'Reilly, 2003). Indeed, neuroimaging studies in young adults have supported this idea using encoding-retrieval similarity (ERS) analyses, which show that reinstatement of patterns of activity from encoding reflect task and category-level information that supports memory accuracy (Gordon et al., 2014). Typically, researchers define episodic reinstatement as the correlation for the BOLD response for a voxel, or multiple voxels within a region, at encoding and retrieval periods for a trial type (e.g., Wing et al., 2015). Neuroimaging studies have also shown that reactivation of event-specific neural patterns, above and beyond category or task reactivation, contribute to successful recollection (Wing et al., 2015).

There are several open questions in the literature relating sleep to episodic memory and underlying neural activity. First, although ERS has been shown to be related to episodic memory performance in young adults (e.g., Wing et al., 2015), there is no research examining the influence of habitual sleep quality. Second, there is evidence suggesting no age-related reduction in category-level (i.e., face vs. scene) reinstatement, but emerging research has shown that older adults demonstrate reduced event-specific neural reinstatement as compared to young adults (for a review, Sommer & Sander, 2021), even after accounting for the strength of category-specific perception/encoding (St-Laurent et al., 2014; Trelle et al., 2020). The correlation between age-related reductions in reinstatement and episodic memory performance provide support for the idea that reduced memory specificity may contribute to age-related memory impairment. However, this age-related reduction in event-specific ERS has not been studied in relation to sleep nor across the adult lifespan sample. Third, previous studies have not investigated neural reinstatement for recombined pairs (i.e., items paired differently from the original encoding pair that should be indicated as new at retrieval), which may be particularly sensitive to age-related differences. With univariate analyses, Trelle and colleagues (2020) found that young adults more strongly recruited the dorsolateral prefrontal cortex when indicating recombined pairs as new than did older adults. This might suggest that there are age-related neural differences in highly controlled memory strategies, namely recall-to-reject. Recall-to-reject is dependent on prefrontal control mechanisms that are greatly impacted by age and disproportionately dependent upon adequate sleep (for reviews: Duarte & Dulas, 2020; Wilckens et al., 2012). Finally, despite well-known racial/ethnic sleep disparities, the association between poor sleep and episodic memory and related brain activity is largely underexplored.

The present study addresses these gaps by recruiting a racially/ethnically diverse adult lifespan sample to assess sleep-memory associations. We collected habitual sleep data for 1 week using wrist-worn accelerometers. This enabled us to measure both average and night-to-night variability in sleep quality and quantity and their contributions to episodic memory. To examine neural similarity between encoding and retrieval, we applied representational similariytsimilarity analysis (RSA) to time-frequency EEG data collected during encoding and retrieval for a paired associate learning task. Numerous studies have shown that oscillatory power in several frequency bands is related to episodic memory performance (for review, Hanslmayr & Staudigl, 2014). Theta synchronization (4–8 Hz) during encoding (Staudigl & Hanslmayr, 2013) and retrieval (Gruber et al., 2013) predicts successful memory performance, consistent with the idea that theta reflects the activity of hippocampo-cortical feedback loop (for a review, Klimesch, 1999). Similarly, alpha (8–12 Hz) and beta (14–30 Hz) desynchronization are associated with successful episodic memory performance (Fellner et al., 2013). Thus, for the current study, we examined oscillatory activity for a wide range of frequencies (4–70 Hz). EEG allows for the examination of neural reinstatement without the limitations of temporal autocorrelation that reduces the separability of individual trials in BOLD data (Mumford et al., 2014). EEG captures specific time periods of encoding that are reinstated during retrieval, offering insight into the processes that might support ERS-related memory benefits. For example, in young adults, neural similarity has been related to episodic memory performance at 500 ms post-stimulus onset (Lu et al., 2015). Memory reinstatement has also been linked with a similar temporal window (400–500 ms) in young adults (Johnson et al., 2015). These time intervals are consistent with univariate ERP research that reflects recollection-based memory retrieval (for a review, Rugg & Curran, 2007).

Here, we assessed event-specific, oscillatory similarity across frequencies between paired associates at encoding and retrieval in racially/ethnically diverse people across the adult lifespan. Considering the association between sleep quality and memory performance in young and older adults (for a review, Mander et al., 2017), we predict that individual differences in memory performance and the degree of ERS will be related to individual differences in sleep quality. We will explore if age or race/ethnicity-related differences in sleep quality contribute to episodic memory performance. Briefly, we find that poor sleep is linked with greater neural similarity for intact pairs that may be tied to familiarity-based memory decisions with, but worse neural similarity for rearranged pairs that may be dependent upon recollection-based memory decisions (Trelle et al., 2020). These findings are in line with the literature showing that recollection-based memories are more sensitive to sleep than familiarity-based ones (Diekelmann et al., 2009). Age and racial/ethnic differences in these findings are discussed.

2. Materials and methods

2.1. Participants

For the present study, we enrolled 108 participants across the adult lifespan from the Georgia Institute of Technology and the Atlanta community. This sample includes data from young and older participants who participated in a previous study (Hokett & Duarte, 2019). Of the 108 participants, 5 were missing sleep data. The remaining 103 participants were considered for inclusion in a principal components analysis (PCA) for the sleep data. Sleep data

Table 1
Participant demographics for each racial/ethnic group

	Racial/Ethnic minority (34)		Non-Hispanic White (39)		Sig.
Measure	Mean	SD	Mean	SD	
Age	38.32	17.73	52.79	21.58	[a]
Education (years)	15.29	1.87	15.51	2.25	
High Confidence *d'*	1.59	0.81	1.33	0.84	
Verbal Fluency (FAS)	43.79	11.04	44.72	11.84	
Visual Recognition	16.88	4.04	16.69	3.89	
Delayed Visual Recognition	17.18	4.071	17.23	3.30	
Verbal Span	26.29	3.42	27.71	2.05	
Sleep Time (Mean)	-0.27	0.87	0.42	0.72	[a]
Sleep Discontinuity (Mean)	0.14	1.14	-0.20	0.78	
Sleep Time (Variance)	0.17	0.84	-0.35	0.84	
Sleep Discontinuity (Variance)	0.06	0.91	-0.20	0.89	[a]
EOD Situations	4.71	2.54	0.64	1.18	[a]
EOD Frequency	11.79	8.82	1.41	2.87	[a]

This table separately shows the demographics for racial/ethnic minorities and non-Hispanic Whites.
Key: EOD , experience of discrimination; SD, standard deviation; Sig., significance.
[a] $p < 0.05$.

for 95 participants were used in the sleep PCA (see section 3.1) after removing 8 outliers (3 SD above or below the mean) for sleep measures. After removing participants who did not have EEG data at both encoding and retrieval or sleep data, 80 participants remained. Of those 80, 6 did not have sufficient numbers of hit or miss EEG trials (7+) at both encoding and retrieval, leaving 74 participants in the experimental sample for the analysis of intact associative memory pairs. For the subsidiary analysis of rearranged pairs, there were 54 participants with sufficient numbers of rearranged correct rejections and false alarms.

Participants in the present sample ranged from 18 to 76 years of age (M = 47; SD = 20; 40 women, 34 men). Participants self-reported their race/ethnicity and were categorized as either non-Hispanic Whites or racial/ethnic minorities for the purposes of this study. One participant did not report any racial/ethnic identity. The participants in the racial/ethnic minority group identified as follows: 24 Black/African Americans, 5 Asians, 3 Hispanic/Latinos, 1 American Indian/Alaska Native, and 1 as multicultural (Asian/White). See Table 1 for participant demographics. All participants self-reported that they were native English speakers, with normal or corrected to normal vision, and right-handed. None of the participants reported uncontrolled psychiatric disorders, neurological disorders, sleep disorders, nor vascular disease. All participants were cognitively normal, and no participant scored 3 SD below the group mean on the experimental memory performance measure, high confidence *d'*. This study was approved by the Georgia Institute of Technology Institutional Review Board.

2.2. Procedure

On the first lab visit, participants were given a battery of standardized neuropsychological tests to assess their cognitive status and an accelerometer (ActiGraph wGT3X-BT) to monitor sleep. After 1 week of wearing the accelerometer, they returned to the lab, and EEG was recorded during encoding and retrieval as they performed an associative memory task (See Fig. 1). Lastly, participants completed questionnaires, including the 21-item version of Depression, Anxiety, and Stress Scale (Lovibond & Lovibond, 1995), and a subset of participants completed an online questionnaire to assess frequency and instances of discrimination using the Experiences of Discrimination (Krieger et al., 2005) measure.

2.3. EEG acquisition and preprocessing

We recorded electrophysiological signals using 32 Ag-AgCl electrodes with an ActiveTwo amplifier system (Biosemi, Amsterdam, Netherlands). Electrode positioning was based on the extended 10–20 system (Nuwer et al., 1998). EEG preprocessing was performed offline using EEGLAB (Delorme & Makeig, 2004), ERPLAB (Lopez-Calderon & Luck, 2014), and FIELDTRIP (Oostenveld et al., 2011) toolboxes. The procedures for preprocessing were based on previous research in our lab and general recommendations (see Cohen, 2014; Hokett & Duarte, 2019). Briefly, the continuous data was downsampled from 512 Hz to 256 Hz, referenced to the average of the left and right mastoids, and band-pass filtered between 0.5 and 125 Hz. Then, the data was epoched to the presentation of the word pair (0 ms) from -1000 to 3500 ms. After the data was epoched, independent components analysis was run separately for each participant and used for artifact detection (e.g., horizontal and vertical ocular movements).

Prior to wavelet decomposition and RSA, each participant's data reflected an $n \times 32 \times 1152$ matrix, with n being the number of trials and each trial included the band-pass filtered EEG signal at 32 electrodes and 1152 time-bins (i.e., the sampling rate of 256 Hz over each 4.5 second trial). Next, each epoch was downsampled from 256 to 40 Hz and transformed into a time-frequency representation using Morlet wavelets (Percival et al., 1993) with 67 linearly spaced frequencies from 4 to 70 Hz. During wavelet transformation, each epoch was reduced to the time range of interest (i.e., 0 ms–3000 ms after onset). As a result, the data dimension changed to n(trials) $\times$ 32 (electrodes) $\times$ 67 (frequencies) $\times$ 120 power values for 120 25 ms time bins (i.e., the sampling rate of 40 Hz over 3 seconds). Then, we divided the electrodes into 4, non-overlapping electrode regions (See Fig. 2**A**). Power values in the 4–70 Hz range were then averaged over the electrodes within each scalp region. We divided the wavelet transforms into 23 250 ms time windows where every consecutive time window overlapped by 125 ms. A summary of these steps is shown in Fig. 2 (see details in Supplemental Method).

2.4. Representational similarity analysis

We next created a vector of log-transformed power values by averaging power within each 250ms time window separately for each frequency value (in 1 Hz increments) from 4 to 70 Hz, separately for each electrode. We then averaged each of these 250ms window power signal averages within an electrode across the electrodes within a scalp region (e.g., right frontal; see Fig. 2). As a result, for each of the 23 250 ms time windows and 4 electrode regions, the "representational pattern" is a vector of 67 (i.e., 4–70 Hz) log-transformed average power values. Next, separately for each scalp region and 250 ms time window, we assessed the de-

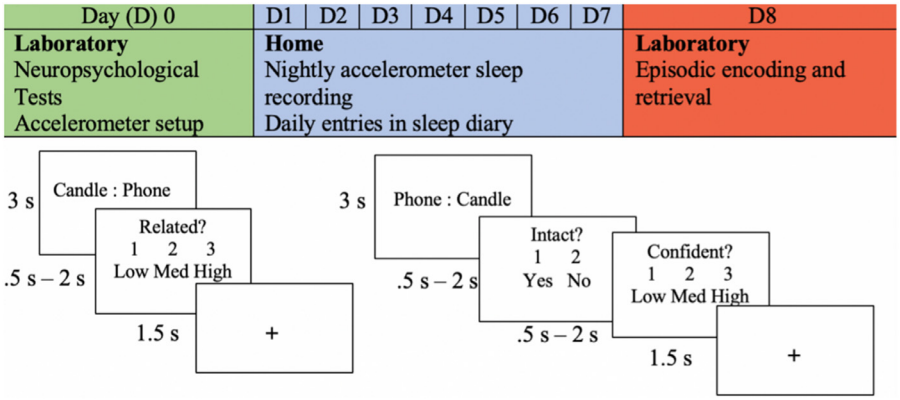

Fig. 1. Experimental procedure as reported in Hokett & Duarte (2019). The encoding session was divided into 4 blocks of 63 trials. To encourage deep encoding and to minimize differing mnemonic strategies, participants were asked to evaluate the similarity (low, medium, or high) between each word pairing. Participants began the intact/rearranged retrieval task shortly after encoding. Intact pairs (168) were presented with the same word as encoding. Rearranged pairs (84) were presented with different words than at encoding. The presentation of the trials was randomized. No new words were presented at retrieval. The retrieval task was divided into 4 blocks, each consisting of 63 trials. Participants were first asked to make an intact/rearranged decision. Then, they were asked to make a confidence decision (low, medium, or high) about their memory decision.

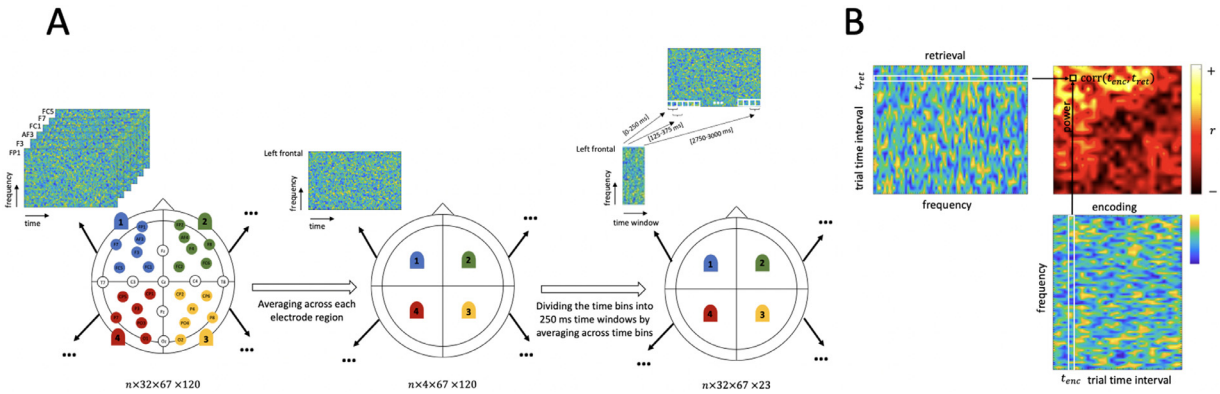

Fig. 2. RSA summary and method. (A) A summary of the preparation steps for RSA. The data size is written at the bottom of each stage. (B) RSA methodology for all time points at encoding and retrieval. For each electrode region, for each of the 23, 250-ms time bins, spaced every 125 ms (50% overlap) we created a feature vector containing log-transformed average power values from 4 Hz to 70 Hz during that time window. These power values were calculated by averaging power across the electrodes in an electrode region and the 10 time bins within a 250 ms time window separately for each frequency from 4 to 70 Hz. The feature vector—the average log-transformed power values from 4 Hz to 70 Hz— from each 250 ms time window in an electrode region corresponding to a trial at encoding (bottom) is correlated with the feature vector from every 250 ms time window for a trial at retrieval (left; rotated by 90°). To illustrate, sample feature vectors of a trial at encoding (t_{enc}) and another trial at retrieval (t_{ret}) are highlighted with a white box. Correlating these 2 feature vectors leads to 1 correlation coefficient, that is, 1 coordinate (shown as the black box) on a matrix with time on both axes. Calculating all pairwise Pearson correlations between the frequency vectors associated with different 250 ms time windows at encoding and retrieval leads to a time–time similarity matrix that represents a temporal map of neural reinstatement between a trial at encoding and a trial at retrieval for all time window combinations. This procedure was repeated for each of the 4 non-overlapping electrode regions for each participant. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

gree of similarity between the frequency vectors for a specific encoding trial with the frequency vectors for a specific retrieval trial. To quantify this similarity in oscillatory power signals between encoding and retrieval (ERS), we calculated the Pearson correlation between each frequency vector for each 250 ms time window from the encoding period with the analogous frequency vector for each 250 ms time window from the retrieval period (shown in Fig. 2B). Using this approach, we measure the correlation of oscillatory power in EEG signals between the encoding and retrieval of a specific trial type for a particular scalp region and time window. This frequency vector approach was adopted from previous research to provide an index of neural reinstatement with high temporal resolution (Yaffe et al., 2014).

For each participant, we computed within-event similarity and between-event similarity for high confidence hits (remembered) and misses (forgotten) for intact pairs. Within-event similarity was computed as described above for a trial at retrieval and its matching trial at encoding (i.e., same word pair). Between-event similarity was computed for a trial at retrieval and the feature vectors associated with all the trials at encoding of the same category (i.e., high confidence hit or miss) that did not share a word with that word pair at retrieval. We also computed the within-event and between-event similarity for correct rejections and false alarms for rearranged events. Within-event similarity was assessed between the feature vectors associated with a given trial at retrieval and the feature vectors associated with the *2 trials* at encoding that shared a word with the rearranged word pair (e.g., apple-paper at retrieval corresponded to apple-window and screen-paper trials at encoding). Between-event similarity was computed between the feature vectors associated with a trial at retrieval and the feature vectors associated with all of the trials at encoding of the same category (i.e., correct rejection or false alarm) that did not share a word with that word pair at retrieval.

Next, we subtracted between-event similarity matrices from within-event similarity matrices for each trial. We then averaged these item-specific, time-time similarity matrices across trials of

the same trial type (e.g., high confidence hits, correct rejections) for each participant, which resulted in average item-specific time-time similarity matrices for each electrode region and trial type. We subtracted event-specific miss similarity from event-specific hit similarity ([within-high confidence hit - between-high confidence hit] - [within-miss - between-miss]) and event-specific correct rejection similarity from event-specific false alarm similarity ([within-correct rejection – between-correct rejection] – [within-false alarm- between-false alarm]). This approach was used to isolate memory-related neural similarity from more general sources of neural similarity.

To assess significant encoding time-retrieval time similarity clusters, time windows with correlations larger than a threshold (associated $p \leq 0.05$) were chosen and combined into contiguous clusters based on the temporal adjacency. For example, if the ([250-500ms] encoding, [500–750 ms] retrieval) and ([375–625 ms] encoding, [500–750 ms] retrieval) are both associated with significant correlation values, they would form a significant cluster of ([250–625 ms] encoding, [500–750 ms] retrieval). To test the significance of each of the new combined temporal clusters, the correlation values were permutated 10,000 times to obtain a null probability distribution of the cluster-based statistics (Maris & Oostenveld, 2007). For all correlation and moderation analyses, neural similarity metrics were restricted to time intervals spanning a minimum of 2 consecutive time windows (i.e., 375 ms) at encoding and retrieval.

2.5. Actigraphy data

The actigraphy data was processed in the same way as reported in Hokett & Duarte (2019). Briefly, we extracted the means and variances (calculated as the squared standard deviation in night-to-night sleep means) for TST, WASO, sleep fragmentation index (SFI), and number of awakenings. TST is a sum of the total minutes spent asleep, and WASO is the sum of minutes spent awake after sleep onset. SFI measures the degree of restlessness during sleep; the number of awakenings is a sum of the awakenings during the sleep period.

2.6. Statistical analysis

In an effort to measure recollection-based memory, which is disproportionately affected by both age and sleep (for reviews: Diekelmann et al., 2009; Duarte & Dulas, 2020), we measured memory performance using *d'* for high confidence hits, (i.e., not including low confidence decisions). Previous research suggests that high confidence memory decisions are more sensitive to age-related differences (Fandakova et al., 2013).

To assess racial/ethnic group differences in sleep quality, memory performance, and ERS, we used analysis of covariance. The independent variable was racial/ethnic group; the dependent variables were entered separately for each model and included sleep quality components and high confidence *d'*. Chronological age was included as a covariate for each model. The PROCESS macro (Hayes, 2018) was used to determine if associations between sleep quality and memory performance were moderated by chronological age or racial/ethnic group (racial/ethnic minorities as compared to non-Hispanic White participants). We also assessed if associations between sleep quality and ERS were moderated by chronological age or racial/ethnic group. Chronological age was added as a covariate for all moderation analyses that assessed racial/ethnic group as a moderator.

We ran 3 types of moderation analyses. First, we assessed age as a moderator for the sleep-memory association at the behavioral level. In the first block, age and sleep quality were included. In the second block, we included the interaction term between age and sleep. Memory performance (*d'*) was the dependent variable. Second, we assessed age as a moderator for associations between sleep quality and ERS. Similarly, age and sleep were included in the first block. In the second block, we included the interaction term between age and sleep quality, and the dependent variable was ERS. Third, moderation was used to assess racial/ethnic group as a moderator for the sleep-ERS association. The structure of the racial/ethnic group moderation analyses was identical to that of the previous type; however, age was included as a covariate for all analyses that included racial/ethnic group given their age differences.

Table 2
Sleep variable loadings for the mean and variance PCA

	Sleep variable	Sleep discontinuity	Sleep time
Mean	Wake After Sleep Onset	**0.935**	-0.184
	Number of Awakenings	**0.892**	0.199
	Sleep Fragmentation Index	**0.790**	-0.485
	Total Sleep Time	-0.036	**0.964**
Variance	Wake After Sleep Onset	**0.782**	0.376
	Number of Awakenings	0.266	**0.805**
	Sleep Fragmentation Index	**0.850**	-0.12
	Total Sleep Time	-0.085	**0.764**

The table shows the loadings for the sleep mean and variance variables of interest. Bold text indicates the dominant variables for each component.

3. Results

3.1. Principal components analysis for sleep variables

To reduce the number of interrelated sleep variables, we used PCA with Varimax rotation using all participants with reliable actigraphy data ($n = 95$). We ran separate PCAs for the sleep means and variances. PCA components were retained if the Eigenvalues were greater than 1. The PCA for the sleep means and the PCA for the sleep variances resulted in 2 components and were used in the following analyses. We will refer to the mean components as sleep discontinuity (awakenings, WASO, SFI) and sleep time (TST). The variance components will be referred to as sleep time variance (TST, awakenings) and sleep discontinuity variance (SFI, WASO; see Table 2).

3.2. Behavioral results

3.2.1. Age-related differences in memory performance and sleep quality

Older age was associated with worse high confidence *d'* ($r(72) = -0.48$, $p < 0.001$), greater sleep discontinuity variance ($r(72) = 0.27$, $p = 0.021$), and reduced sleep time variance ($r(72) = -0.312$, $p = 0.007$). This indicates that sleep time is more consistent across nights with older age, but there is greater night-to-night variability in the continuity of sleep with older age. Age was not associated with either of the mean sleep components (*p's* > 0.746).

Moderation analyses demonstrated that the association between sleep time variance and high confidence *d'* increased with age ($\Delta R2 = 0.05$, $F(1, 70) = 5.19$, $p = 0.026$), such that those older adults with more variable sleep time had the lowest memory performance. Fig. 3A presents the simple slopes for the moderation effects. Age was not a significant moderator for the sleep-memory association for any of the other 3 sleep components (*p's* > 0.054).

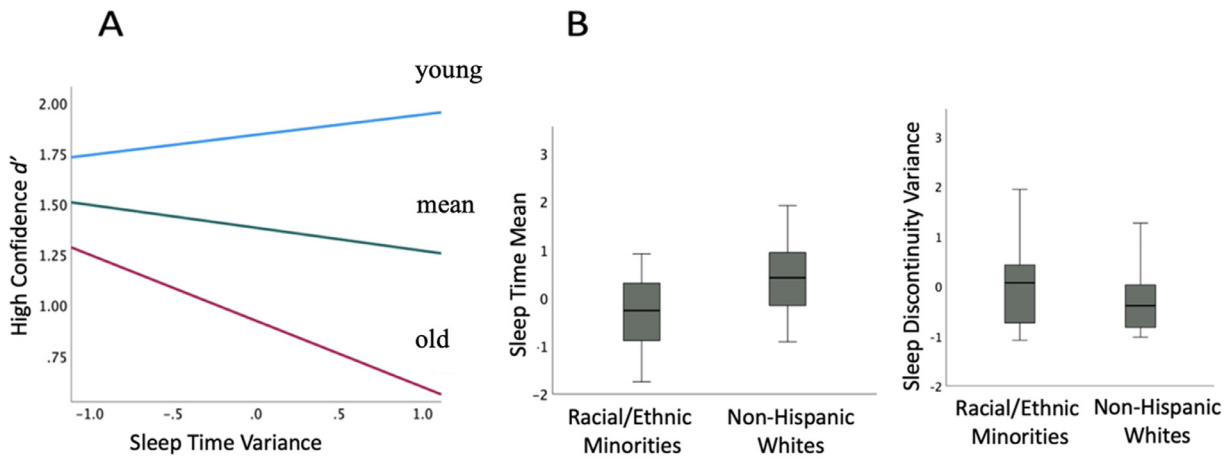

Fig. 3. Age and Racial/Ethnic Group Differences in Sleep and Memory. (A) Sleep Quality x Memory Performance with Age as a Moderator. The lines represent age: - 1 SD (blue) = young, mean (green), and + 1 SD (red) = old. (B) Boxplot of racial/ethnic group differences in sleep quality for mean sleep time and sleep discontinuity variance. The black bar within the gray box depicts the median for each group. The lower edge of the gray box shows the first quartile, and the upper edge shows the third quartile. The error bars illustrate the minimum and maximum sleep quality values. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.2.2. Racial/ethnic group-related differences in memory performance and sleep quality

Since the racial/ethnic minority group was significantly younger than the non-Hispanic White group (see Table 1), we measured racial/ethnic group differences using analysis of covariance, controlling for chronological age. For each ANCOVA, racial/ethnic group was entered as the independent variable, one of the 4 sleep components was entered as the dependent variable, and chronological age was added as a covariate.

There were no differences between racial/ethnic minorities and non-Hispanic Whites for high confidence *d'* ($F(1, 70) = 0.01$, $p = 0.920$, $\eta_p^2 < 0.000$). As seen in Fig. 3B, racial/ethnic minorities had worse sleep than non-Hispanic Whites as indicated for both mean sleep time ($F(1, 70) = 17.16$, $p < 0.000$, $\eta_p^2 = 0.197$) and sleep discontinuity variance ($F(1, 70) = 5.15$, $p = 0.026$, $\eta_p^2 = 0.069$). There were no other statistically significant differences in sleep nor sleep-memory associations between the racial/ethnic groups (*p's* > 0.066).

Given the association between race-related stress and sleep disparities in the literature (for a review, Slopen et al., 2016), as a follow-up, we examined events of discrimination in a subsample of 40 participants who completed the experiences of discrimination questionnaire (see Method). Racial/ethnic minorities reported more instances of discrimination (i.e., number of situations; $t(21.29) = 6.11$, $p < 0.001$) and a greater frequency of discrimination than non-Hispanic Whites ($t(18.63) = 4.67$, $p < 0.001$). Importantly, instances of discrimination and the frequency of discrimination correlated with reduced mean sleep time when controlling for chronological age ($r(37) = -319$, $p = 0.048$; $r(37) = -0.338$, $p = 0.036$, respectively). There were no other significant correlations between sleep quality and discrimination (absolute *r's* < 0.23, *p's* > 0.166)

3.3. EEG results

For all subsequent analyses, we used the sleep time variance component, as it was the variable that showed sensitivity to memory performance (see Behavioral Results). As described in the Method, we computed correlations between sleep time variance and event-specific ERS for intact (within-high confidence hit - between-high confidence hit) - (within-miss - between-miss) and rearranged paired associates (within-correct rejection – between-correct rejection) - (within-false alarm- between-false alarm), respectively. As predicted by prior fMRI studies, we found associations between older age and low ERS (St-Laurent et al., 2014; See Supplemental Results). The sleep-ERS results are reported in the section below. To assess if these results varied by temporal or spatial RSA parameters, we assessed the same analyses across different temporal and spatial parameters, presented in Supplemental Results.

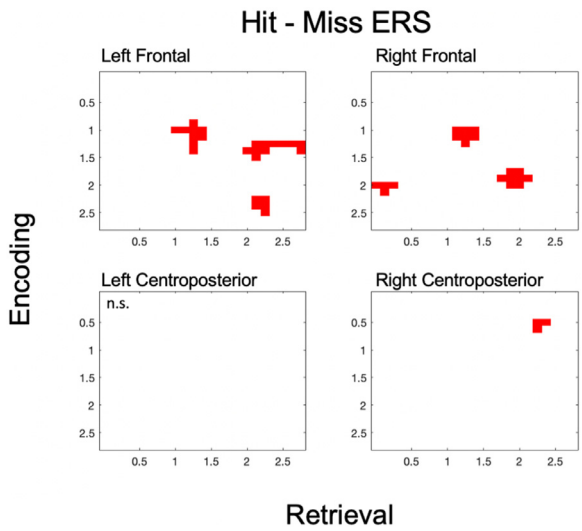

Fig. 4. ERS time-time clusters for intact pairs showing correlations with sleep across racial/ethnic group. Each figure illustrates the time intervals for significant correlations between sleep time variance and event-specific ERS for each encoding (y-axis) and retrieval (x-axis) time interval (in seconds). Clusters with positive correlations are shown in red. n.s., not significant/no significant clusters. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.3.1. Intact pairs

We first assessed correlations between sleep time variance and event-specific ERS for intact paired associates, across age and racial/ethnic group. We found 7 significant clusters. These clusters are shown in Fig. 4. See Table 3 for the electrode regions, time intervals, partial *r* statistics (correcting for age), and *p*-values for

Table 3
Intact ERS clusters showing associations with sleep time variance

Region	Encoding interval (ms)	Retrieval interval (ms)	Partial *r*	*p*
Left frontal	875–1625	1000–1625	0.36[a]	0.002
Left frontal	1250–1750	2000–3000	0.334[a]	0.004
Left frontal	2250–2750	2125–2500	0.325[a]	0.005
Right frontal	2000–2375	0–500	0.261[a]	0.026
Right frontal	1000–1500	1125–1625	0.278[a]	0.017
Right frontal	1750–2250	1750–2375	0.339[a]	0.003
Right centroposterior	500–875	2250–2625	0.259[a]	0.027

Chronological age was included as a covariate for these analyses.
[a] $p < 0.05$.

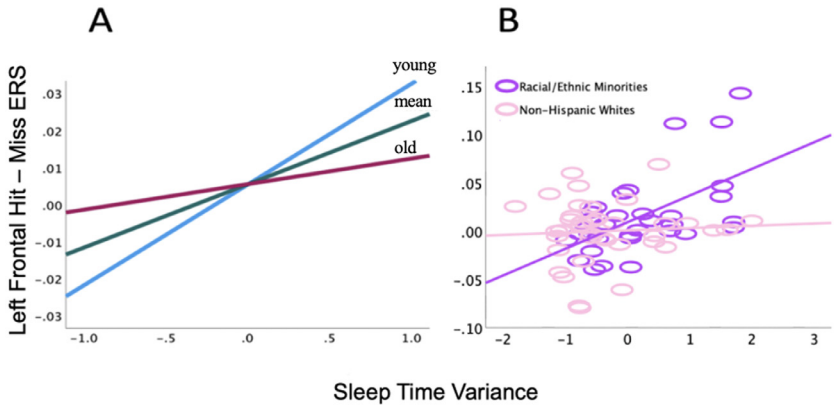

Fig. 5. Greater sleep time variance associated with greater left frontal ERS for intact pairs. (A) The lines represent age: - 1 SD (blue) = young, mean (green), and + 1 SD (red) = old. Younger age is more strongly associated with greater ERS and greater sleep time variance. This relationship is reduced with age. (B) Left frontal ERS is on the y-axis, and sleep time variance is on the x-axis. Racial/ethnic minorities (purple ovals) show a stronger, positive relationship between sleep time variance and ERS than non-Hispanic White adults (pink ovals). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

each significant cluster. Generally, greater sleep time variance was associated with greater ERS for intact pairs.

Next, we examined if associations between sleep time variance and ERS varied by age or racial/ethnic group using moderation analyses. Age significantly moderated the association between sleep time variance and ERS, such that younger age was associated with a stronger, positive association between sleep time variance and intact pair ERS (encoding interval: 875–1625 ms; retrieval interval: 1000–1625 ms; ($\Delta R2 = 0.06$, $F(1, 70) = 5.32$, $p = 0.024$; See Fig. 5A). Moreover, controlling for chronological age, racial/ethnic group was a significant moderator for this association for the same cluster ($\Delta R2 = 0.09$, $F(1, 68) = 7.65$, $p = 0.007$; Racial/ethnic minorities: *partial* $r(31) = 0.58$, $p < 0.001$; non-Hispanic Whites = *partial* $r(36) = 0.07$, $p = 0.661$; See Fig. 5B). To ensure that this effect was not driven by the age difference between racial/ethnic groups, we conducted an additional analysis with a subset of participants to match chronological age across groups. The racial/ethnic group moderation effect remained statistically significant within the age-matched sample ($\Delta R2 = 0.07$, $F(1, 60) = 5.14$, $p = 0.027$). There were no other significant moderation effects (*p's* > 0.140). Overall, greater sleep time variance was associated with greater ERS for intact pairs, particularly with younger age and in racial/ethnic minorities, across age.

3.3.2. Rearranged pairs

Nine significant electrode clusters were identified that showed reliable correlations between rearranged pair ERS and sleep time variance, across age and racial/ethnic group. These clusters are shown in Fig. 6 and Table 4. For most electrode clusters, greater sleep time variance was associated with lower event-specific ERS for rearranged paired associates.

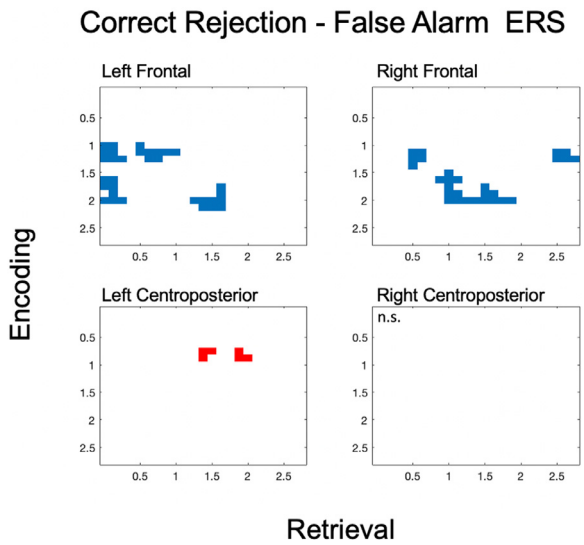

Fig. 6. ERS time-time clusters for rearranged pairs showing time intervals for significant correlations with sleep time variance across racial/ethnic group. Each figure illustrates the correlation between sleep time variance and event-specific ERS for each encoding (y-axis) and retrieval (x-axis) time interval (in seconds). Clusters with positive correlations are shown in red, and those with negative correlations are shown in blue. n.s., not significant/no significant clusters. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

To examine if the strength of the sleep-ERS association varied by age or racial/ethnic group, we employed moderation analyses. There were no statistically significant moderation effects of age or racial/ethnic group for the association between sleep time vari-

Table 4
Rearranged ERS clusters showing associations with sleep time variance

Region	Encoding interval (ms)	Retrieval interval (ms)	Partial *r*	*p*
Left frontal	1000–1500	0–500	-0.399	0.003
Left frontal	1625–2250	0–500	-0.376	0.006
Left frontal	1000–1500	500–1250	-0.368	0.007
Left frontal	1750–2375	1250–1875	-0.385	0.004
Right frontal	1125–1625	500–875	-0.342	0.012
Right frontal	1500–2250	875–2125	-0.423	0.002
Right frontal	1125–1500	2500–3000	-0.381	0.005
Left centroposterior	750–1125	1375–1750	0.314	0.022
Left centroposterior	750–1125	1875–2250	0.34	0.013

Chronological age was included as a covariate for these analyses.
[a]$p < 0.05$.

ance and ERS for rearranged pairs (p's $>$ 0.161), suggesting that this effect may be consistent across the adult lifespan and across racial/ethnic groups.

4. Discussion

The findings of the present study are the first to show associations among age, racial/ethnic group, sleep quality, memory performance, and episodic neural reinstatement. In the present lifespan sample, we found that racial/ethnic minorities had poorer sleep quality and higher experiences of discrimination than non-Hispanic White adults, which was associated with worse sleep quality. Furthermore, the association between more varied, night-to-night sleep quality and poor episodic memory performance strengthened with older age. Interestingly, sleep variability was positively associated with greater ERS for intact pairs, particularly for racial/ethnic minorities and for younger adults. By contrast, sleep variability was associated with lower ERS for rearranged pairs, regardless of age or race/ethnicity.

4.1. More variable sleep is associated with poorer memory, particularly with older age

Consistent with prior studies, older age was related to more varied sleep quality, including sleep fragmentation and WASO, but more consistent sleep duration (Shoji et al., 2015). Furthermore, those with more variable sleep duration had worse memory performance, and this association was stronger with older age. This finding conflicts with some previous research showing stronger associations between slow wave sleep duration and cued recall memory performance in young adults than older adults (Scullin, 2013). In contrast, other studies that examined habitual sleep quality (e.g., WASO), found stronger sleep-recall associations in older adults than young adults (Mary et al., 2013). Thus, the strength of sleep-memory associations across age may differ according to sleep index. Specifically, we speculate that while memory performance in young adults is more sensitive to average neural indices of sleep (e.g., slow wave sleep), memory performance in older adults may be particularly sensitive to night-to-night fluctuations in sleep quality (for a review, Hokett et al., 2021).

4.2. Racial/ethnic minorities sleep more poorly than non-Hispanic White adults

Consistent with previous epidemiology studies, racial/ethnic minorities had reduced sleep duration and more varied, night-to-night sleep quality than non-Hispanic White adults (for reviews: Bei et al., 2016; Johnson et al., 2019). Moreover, reduced sleep duration was correlated with more experiences of discrimination, which aligns with findings from previous research using subjective sleep measurements (for a review, Slopen et al., 2016). Although the current study was cross-sectional, longitudinal work suggests that stress predicts poorer sleep quality (Hall et al., 2015). Interestingly, memory performance and the association between sleep variance and memory performance were statistically equivalent across racial/ethnic groups. However, as discussed below, racial/ethnic differences were evident in the strength of associations between sleep and the episodic memory reinstatement.

4.3. Associations between sleep and ERS

Successful episodic memory retrieval is thought to depend upon the reinstatement during event retrieval of neural activity patterns and associated operations present during encoding (Norman & O'Reilly, 2003). Here, we used EEG to identify episodic neural reinstatement effects that were sensitive to word pair-specific activity patterns, above and beyond cognitive operations commonly engaged across event types (e.g., effort, semantic processing).

Similar to other EEG studies investigating the time course of episodic reinstatement, we found that encoding and retrieval activity were correlated within similar time intervals. However, we also observed significant asymmetrical ERS effects in which encoding activity was similar to retrieval activity occurring either earlier or later. There are a few possible explanations for these asymmetrical ERS patterns. Encoding-related activity, and related cognitive operations, may last longer during encoding than retrieval, resulting in later time intervals at encoding correlating with earlier ones at retrieval. This explanation is consistent with findings showing that episodic reinstatement occurs on a temporally compressed timescale relative to encoding (Yaffe et al., 2014). Another, non-mutually exclusive possibility is that some earlier occurring encoding processes (e.g., perception) are reinstated later during retrieval perhaps during attempts to recall prior word pairs in order to reject rearranged ones (Jafarpour et al., 2014). Regardless of the specific mechanisms underlying these symmetrical and asymmetrical reinstatement effects, the current results show that they are similarly related to sleep quality.

4.3.1. Association between sleep and ERS differs for intact and rearranged pairs across age

For intact word pairs, we found that greater night-to-night sleep time variance was related to greater ERS. In contrast, for rearranged pairs, we found the opposite association – greater sleep variance was associated with reduced ERS. The negative association between sleep quality and intact pair ERS was not expected, as we hypothesized better sleep quality to be associated with stronger associative memory, reflected by greater ERS for successful than unsuccessful memory trials for both intact and rearranged pairs. One possible explanation for these results could be related to dif-

ferential contributions of familiarity and recollection to associative recognition for intact and rearranged pairs, respectively. Memory for rearranged pairs is thought to reflect recall-to-reject based memory processes (for a review, Rotello, 2001). That is, participants may try to recall the previously presented pair during the encoding episode (e.g., apple-ball) to correctly reject the newly combined pair at retrieval (e.g., apple-spoon). By contrast, intact pairs may be recognized on the basis of recollection of pair-specific details, or on the basis of familiarity in the absence of these details, particularly when the items can be unitized (e.g., orange-cat; Quamme et al., 2007). Although we did not instruct participants to unitize the pairs, it is possible that they may have at least sometimes done this spontaneously. Further, although neural reinstatement has typically been thought to support recollection-based memory, some evidence shows it may also be observed for familiarity-based memory judgements (Johnson et al., 2009). Thus, it is possible the intact pair ERS effects reflect, at least to some extent, familiarity-based memory processes.

Recollection-based memory judgments generally show stronger sleep-related effects than familiarity-based memory ones (for a review, Diekelmann et al., 2009). For example, participants who sleep following an encoding task tend to perform significantly better on recollection-based memory tasks as compared to those who remain awake (Atienza & Cantero, 2008). Interestingly, these studies have shown no differences between sleep and wake groups for familiarity-based recognition. The authors posited that since recollection-based memory is hippocampus-dependent, the lack of sleep disrupts the hippocampal replay that strengthens recollection-based memories (Atienza & Cantero, 2008). If rearranged pairs are successfully rejected due to employment of recollection-related processes (i.e., recall-to-reject), we speculate that participants with more variable sleep quality may have been able to make use of familiarity to a greater extent than recollection to support their associative memory performance. Behaviorally, older adults showed stronger associations between greater sleep time variance and lower d' than young adults did. We expect that high confidence *d*' and ERS for rearranged pairs are based more on recollection than familiarity memory. Our results suggest that sleep sensitivity to recollection-based memory retrieval is particularly strong in old age. However, these conclusions require further investigation using a task specifically designed to separate recollection from familiarity (e.g., remember/know).

4.3.2. Sleep-ERS associations are moderated by age

We found that the association between sleep time variance and intact pair late frontal ERS was moderated by chronological age, such that younger age demonstrated the strongest associations between sleep time variance and ERS. Prior EEG research has shown similar event-specific neural reinstatement over frontal regions in young adults (Yaffe et al., 2014). The present results are also consistent with ERP research. The late time course of the frontal ERS effects observed here is reminiscent of late onsetting, sustained frontal ERPs that have been shown to distinguish recollected events based on their study task history or associated perceptual context (i.e., face vs. scene context; Johnson et al., 2008). A plausible interpretation of these frontal ERS effects is that they reflect PFC-dependent post-retrieval monitoring operations including the maintenance, manipulation, and evaluation of retrieved memory representations in the service of a response (for a review, Rugg, 2004).

Considering that older adults are more likely to rely on familiarity than are younger adults (for a review, Duarte & Dulas, 2020), we might have expected the sleep-intact pair ERS association to be *stronger* with older age. However, the stronger association between sleep quality and ERS with younger age is likely because of reduced variance in ERS with older age. As mentioned above, we found that older age was associated with reduced ERS. Low variation in ERS in older adults may have obscured our ability to detect significant associations with sleep. Thus, reduced range could explain the insignificant effect between sleep and ERS in old age as compared to younger age. Future research should assess the association between sleep variance and ERS in larger participant samples with more variable ERS.

4.3.3. Sleep-ERS associations are moderated by race/ethnicity

We found a moderation effect of racial/ethnic group in which ERS for intact pairs was more sensitive to sleep variance for racial/ethnic minorities than non-Hispanic Whites. This finding is consistent with our previous research demonstrating a stronger association between poorer sleep quality and reduced memory-related neural activity in Black adults than White adults using univariate EEG analysis (Hokett & Duarte, 2019). In addition to poorer sleep quality, racial/ethnic minorities reported greater instances and frequency of discrimination. Although speculative, greater discrimination in combination with poorer sleep quality may to contribute to greater reliance on familiarity-based as compared to recollection-based memory retrieval. Both poor sleep and high stress have been linked with poor episodic memory performance, including reduced recollection of episodic de tails (Atienza & Cantero, 2008; Gagnon et al., 2019). Chronic stress, imposed by recurrent experiences of discrimination, may be linked with functional and structural changes in the hippocampus and thereby influence greater reliance on familiarity-based episodic memory retrieval (for a review, Kim et al., 2015). Taken together, more varied sleep quality may be linked to greater familiarity-based memory retrieval, and this effect may be particularly strong in young adults and racial/ethnic minorities.

4.4. Strengths and limitations

The present study has several strengths, including an adult lifespan sample of racially/ethnically diverse participants, multi-night, sleep quality measurement, and event-specific ERS analysis for intact and rearranged pairs. The results of our ERS analysis indicate differential associations between sleep and memory-supporting mechanisms. However, this study is not without limitations. The sample size for the rearranged analysis was reduced (54 people) because of the lower trial numbers for rearranged pairs, which could have inflated the results for the rearranged pairs. It is also important to note that the racial/ethnic minority group was heterogeneous, and sleep disparities may differ by race/ethnicity (Johnson et al., 2019). Also, the racial/ethnic group was significantly younger than the non-Hispanic White group. However, we controlled for chronological age where appropriate.

Further, no new pairs were included in the experimental task and as such, we cannot separate item from associative recognition. It is possible that the larger ERS for intact pair hits than misses reflects both greater associative and greater item recognition. However, we do not believe that the contrast between rearranged correct rejections and false alarms is similarly confounded for 2 reasons. First, if correctly rejected rearranged pairs reflected item recognition failures instead of recollected rearranged pairs, it seems unlikely that episodic reinstatement would be larger for correct rejections than false alarms (i.e., item recognition successes), which was the pattern we found in all significant clusters. Second, individuals with more variable sleep quality showed smaller rearranged pair ERS effects. This pattern seems more in line with greater associations between higher sleep consistency and greater ERS being related to evidence of successfully recollected rearranged pairs than to item recognition failures.

4.5. Conclusion

Our results suggest that consistent sleep may be particularly important for those who are older and racial/ethnic minorities, as the associations between sleep and memory were particularly strong for these groups. People with more variable sleep quality may rely on familiarity for memory retrieval to a greater extent than those with more consistent sleep. Greater sleep variance may be linked with lower ability to recollect specific details about past events. Future research should investigate these findings in larger, racially/ethnically diverse people across the lifespan to assess generalizability to more specific racial/ethnic minority groups.

Disclosure statement

The authors declare no conflicts of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neurobiolaging.2022.04.015.

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