





Load-dependent modulation of alpha oscillations during working memory encoding and retention in young and older adults

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Abstract

Working memory (WM) is vulnerable to age-related decline, particularly under high loads. Visual alpha oscillations contribute to WM performance in younger adults, and although alpha decreases in power and frequency with age, it is unclear if alpha activity supports WM in older adults. We recorded electroencephalography (EEG) while 24 younger (aged 18–35 years) and 30 older (aged 50–86) adults performed a modified Sternberg task with varying load conditions. Older adults demonstrated slower reaction times at all loads, but there were no significant age differences in WM capacity. Regardless of age, alpha power decreased and alpha frequency increased with load during encoding, and the magnitude of alpha suppression during retention was larger at higher loads. While alpha power during retention was lower than fixation in older, but not younger adults, the relative change from fixation was not significantly different between age groups. Individual differences in alpha power did not predict performance for either age groups or at any WM loads. We demonstrate that alpha power and frequency are modulated in a similar task- and load-dependent manner during WM in both older and younger adults when WM performance is comparable across age groups.

Impact statement: Aging is associated with a marked decrease in the power and frequency of alpha oscillations. Here, we demonstrate that when verbal working memory performance is matched across age groups, alpha power and frequency are modulated in a similar task- and load-dependent manner in both young and older adults.

KEYWORDS

alpha oscillations, cognitive aging, EEG, working memory

1 | INTRODUCTION

Verbal working memory (WM), the ability to actively maintain and/or manipulate verbal information to guide immediate cognitive processing (Baddeley, 1992), is vulnerable to age-related decline. Compared to younger adults, healthy older adults are able to store fewer items in WM, are less able to manipulate those items (Fisk & Warr, 1996), and are

more susceptible to interference from distracting information (Gazzaley and D'Esposito, 2007). This age difference is particularly salient under high WM demands, with older adults demonstrating poorer performance with higher loads relative to younger adults (McEvoy et al., 2001; Wild-Wall et al., 2011). Despite this, the neural mechanisms underlying such age differences at varying WM loads are not well understood.

Advancing age is associated with progressive changes in the frequency and power of neural oscillations (Klass & Brenner, 1995; Klimesch, 1999). Alpha (~8–12 Hz) is perhaps the most affected frequency band in aging, with alpha oscillations significantly lower in magnitude and slower in frequency in healthy older adults compared with younger adults at rest (Babiloni et al., 2006; Klimesch, 1997; Lindsley, 1939). As alpha oscillations in posterior brain regions are thought to support WM performance (Klimesch, 2012), age-related changes to alpha activity may underlie WM performance deficits in healthy older adults.

WM is typically divided into three stages: encoding, retention, and retrieval (Baddeley, 1992). Most of the research in this area has focused on the retention period, with a large body of evidence suggesting that alpha is modulated during this stage, though the location, direction, and magnitude of this change depends on the type of task. Using modified Sternberg tasks, it has been reliably shown that alpha power increases in visual brain areas during retention, particularly under higher WM loads (Jensen et al., 2002; Meltzer et al., 2008; Proskovec et al., 2019). The predominant interpretation of this finding is that alpha activity reflects a suppression of sensory input from the visual stream to prevent disruption to WM maintenance occurring in frontal brain regions (Jensen & Mazaheri, 2010). In lateralized WM tasks where subjects attend to and memorize the information in one hemifield, and ignore the other, parieto-occipital alpha power decreases in the task-relevant, and increases in the task-irrelevant hemisphere (Sauseng et al., 2009). Finally, alpha suppression with increasing WM load in parieto-occipital sites has been reported in n-back style paradigms (Gevins et al., 1997; Krause et al., 2000; Pesonen et al., 2007; Stipacek et al., 2003) and delayed match-to-sample tasks (Fukuda et al., 2015). Less is known about the alpha oscillatory dynamics underlying the WM encoding period, although posterior alpha power has been shown to decrease in this stage, likely reflecting attentional processes (Heinrichs-Graham & Wilson, 2015). Likewise, alpha frequency has been linked to WM performance as a trait variable at rest (Klimesch, 1999) and during task performance in younger adults (Haegens et al., 2014).

Much of the research investigating age and load-related changes in alpha activity during WM have involved lateralized, visual WM tasks. In a study involving a hemifield change detection task with spatial cueing, it was found that while younger adults demonstrated higher alpha power ipsilateral to the attended hemifield during the retention period at medium and high loads, older adults only showed lateralization at medium loads. This suggests that inhibitory processes indexed by alpha power modulation are not present in older adults when task difficulty increases (Sander et al., 2012). Likewise, a study employing a hemifield change detection task with an alerting cue showed that older adults had reduced

alpha amplitude lateralization during the retention period compared with younger adults, though between-load differences in alpha lateralization did not predict performance at high WM loads in each age group (Tran et al., 2016). Lastly, using a lateralized delay match-to-sample paradigm with spatial cueing, it was found that at matched WM difficulty, alpha lateralization during retention was minimal in older adults due to bilateral reductions in alpha power, while younger adults demonstrated lower alpha power contralateral to the attended hemifield (Leenders et al., 2018).

However, as the aforementioned studies involved visual WM tasks and a lateralized approach, and the majority of prior work investigating alpha activity during WM using Sternberg tasks have only included younger adults, it is unclear whether alpha activity contributes to verbal WM performance in older adults. A recent study employing magnetoencephalography during a high load (6-letter) modified Sternberg task reported that increases in visual alpha power during the WM maintenance period were present in both older and younger adults (Proskovec et al., 2016). However, relative to younger subjects, the increase in alpha activity was more rapid, widespread, and persistent for longer in older adults, which was interpreted to reflect a compensatory mechanism to aid WM performance in older age (Proskovec et al., 2016). However, as WM load was not manipulated in this study, it is unclear whether older adults modulate visual alpha activity in order to facilitate verbal WM performance under varying WM loads. Likewise, while previous studies have found evidence for task- and load-related alpha frequency modulation during WM, these studies have only involved younger adults (Babu Henry Samuel et al., 2018; Haegens et al., 2014).

In the present study, we investigated the age-related differences in visual alpha activity during verbal WM in response to increasing memory load. We applied a modified Sternberg task with 1-letter, 3-letter, and 5-letter load conditions where WM processes were temporally delineated, in order to identify the alpha oscillatory dynamics underlying the WM encoding and retention stages. We ensured that any observed changes in the power of alpha oscillations were not due to age-related changes in peak alpha frequency by matching power measurements to individual alpha peaks. We sought to test the following hypotheses. First, older adults will show greater performance deficits at higher WM loads than younger adults. Second, older adults will show increased load-dependent modulation of visual alpha power during WM encoding and retention compared to younger adults. Third, age-related differences in visual alpha power during WM will correlate with task performance. Finally, cognitive reserve refers to the ability to maintain cognitive function in the presence of age-related changes to the brain, and can be acquired through socially and cognitively enriching activities throughout the lifetime (Barulli & Stern, 2013). As a secondary aim, we investigated whether cognitive reserve in older

adults was associated with WM performance and alpha activity during the task.

2 | METHOD

2.1 | Participants, demographics, and cognitive reserve

About 24 younger adults (mean age: 23.2 years, *SD*: 4.60, range: 18–35 years, 8 male) and 30 older adults (mean age: 62.7 years, *SD*: 9.09, range: 50–86 years, 17 male) participated in the study. The samples in each group were not significantly different for years of education (older adults: *M* = 15.87 years, *SD* = 4.45 years; younger adults: *M* = 15.71 years, *SD* = 1.97 years, $t_{43,51} = 0.182$, $p = .857$). All older adults were without cognitive impairment (Addenbrooke's Cognitive Examination score (ACE-III) > 82) (Mioshi et al., 2006). Exclusion criteria were a history of neurological or psychiatric disease, use of central nervous system altering medications, history of alcohol/substance abuse, uncorrected hearing/visual impairment, and an ACE-III score of less than 82. All participants gave informed written consent before the commencement of the study, and the experiment was approved by the University of Adelaide Human Research Ethics Committee.

Cognitive reserve (CR) was calculated for each older adult participant by z-transforming their total years of education

and scores on the National Adult Reading test (NART), which is used to estimate verbal IQ (Blair & Spreen, 1989). The z-scores were then averaged to form a cognitive reserve score, and participants were divided into high and low cognitive reserve groups using a median split.

2.2 | Working memory task

The modified Sternberg WM task used stimuli presented by PsychoPy software (Peirce, 2007) (Figure 1). At the beginning of each trial, the participant fixated on a cross in the center of the screen for 2 s. A memory set consisting of either 1, 3, or 5 consonants was then shown for 1 s, followed by a 4 s retention period. For load-1 and load-3 trials, the consonants were presented centrally, with filler symbols (#'s) added to maintain equal sensory input for each condition. A probe letter was then shown, and the subject was instructed to press the right arrow key on a standard keyboard if the letter was in the memory set, or the left arrow key if it was not. The probe remained on the screen until the subject responded. Probe letters were present in the memory set at 50% probability. Participants received a practice block of 20 trials to familiarize themselves with the task, before performing 20 blocks of 15 trials, yielding 300 trials overall (i.e., 100 trials per load). Each block contained an equal number of trials for each load, presented pseudorandomly, and a short break was allowed between blocks.

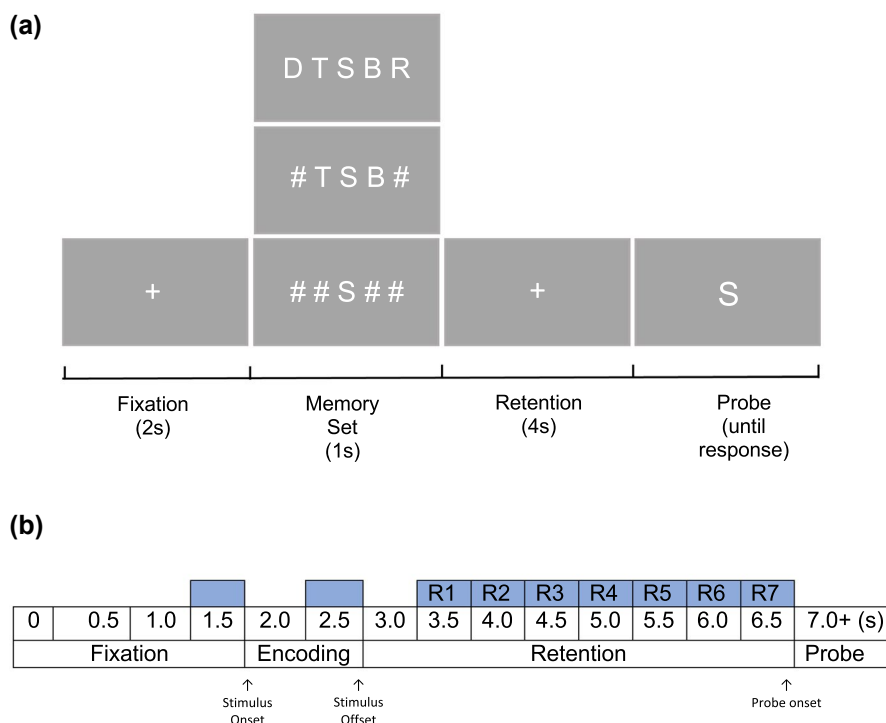


FIGURE 1 (a) Modified Sternberg WM task. Each trial contained four stages, including fixation lasting for 2 s; encoding, where a 1, 3, or 5 load memory set was displayed for 1 s; a 4 s retention stage and a retrieval stage where the subject responded to whether the probe was part of the memory set. (b) Schematic for EEG analysis periods (shown in blue) for fixation, encoding, and retention

To quantify WM performance, reaction time (RT) for correct trials and WM capacity were calculated for each load condition. The participants' WM capacity was quantified using Cowan's K (Cowan, 2001), defined by $K = \text{set size} \times (\text{hit rate} - \text{false alarm rate})$.

2.3 | EEG data acquisition

EEG data were recorded from a 64 channel cap containing Ag/AgCl scalp electrodes arranged in a 10–10 layout (Waveguard, ANT Neuro, Enschede, The Netherlands) using a Polybench TMSi EEG system (Twente Medical Systems International B.V, Oldenzaal, The Netherlands). Due to technical issues, data from the mastoids were not able to be recorded, and as such, data were recorded from 62 channels. Conductive gel was inserted into each electrode using a blunt-needle syringe in order to reduce impedance to < 5 k Ω . The ground electrode was located at AFz. Signals were amplified 20x, online filtered (DC–553 Hz) and sampled at 2048 Hz. Due to the lack of data from the mastoids, data were referenced to the average of all electrodes. EEG was recorded during each block of 15 trials of the WM task.

2.4 | Data pre-processing

Task EEG data were pre-processed using EEGLAB (Delorme & Makeig, 2004) and custom scripts using MATLAB (R2018b, The Mathworks, USA). Each block of EEG data was merged and incorrect trials, as well as trials with outlier RT (defined as $> 3 \times \text{SD}$) were flagged for removal at the epoch stage.

Noisy and unused channels were then removed based on visual inspection, with an average of two channels removed from each age group (range old: 1–5, range young: 1–7). The data were then band-pass (1–100 Hz) and band-stop (48–52 Hz) filtered using zero-phase fourth-order Butterworth filters, down-sampled to 256 Hz and epoched –6 s to 1 s relative to the beginning of the probe. Only correct trials were included in further analysis. Independent component analysis (ICA) was then conducted using the FastICA algorithm (Hyvärinen & Oja, 2000), with the “symmetric approach” and “tanh” contrast function to remove artifacts resulting from eye-blinks and persistent scalp muscle activity. Data were then checked for remaining artifact via visual inspection and trials were removed if necessary (e.g., remaining blinks, non-stereotypic artifacts). Remaining trials were then split according to memory load condition.

After removing trials due to incorrect answers, outlier RTs or excessive artifact, on average, 254 trials were accepted in the final analysis for younger adults (range 171–294). About 85 trials were retained in load-1 and load-3 and 84 in load-5.

An average of 270 trials were accepted for final analysis for older adults (range 198–297). About 273 trials were retained in load-1 and load-3, and 267 in load-5. A mixed effects linear model revealed a significant difference in the number of remaining trials across age groups $F_{1,52} = 9.0$, $p = .04$, but not across WM loads $F_{2,104} = 2.8$, $p = .07$, nor an age by load interaction, $F_{2,104} = 0.7$, $p = .50$.

2.5 | Spectral analysis

FieldTrip toolbox (Oostenveld et al., 2011) was used to analyze task EEG data. Time frequency representations of power to a 0.5 Hz frequency resolution were performed using a multi-taper time-frequency transformation based on multiplication in the frequency domain, a time window three cycles long and a Hanning taper. Power was calculated for individual trials before averaging for each load condition. The first 0.5 s of the encoding and retention periods were excluded to avoid spectral contributions from stimulus evoked responses to the memory set (Figure 1b) (Babu Henry Samuel et al., 2018; Wang & Ding, 2011).

To account for age-related slowing of alpha (Klimesch, 1999), the alpha band frequency range was defined for each participant based on their peak alpha frequency at each stage of the task (fixation, encoding, and retention) and for each load. Alpha frequency range was defined as 2 Hz above and below the peak frequency between 6 and 13 Hz (Klimesch, 1999). Alpha power was then averaged over this frequency range and across parieto-occipital and occipital electrodes (PO7, PO5, PO3, POz, PO4, PO6, PO8, O1, Oz, and O2) at each WM stage (fixation, encoding, and retention; Figure 1b), as well as during each 0.5 s segment of the retention period.

2.6 | Statistical analyses

Statistical analyses were performed using R version 3.4.2. Mixed effects linear models were used to analyze the behavioral and neurophysiological data. For behavioral data, performance (RT or Kc) was the outcome variable, WM load, and age were fixed effects and subjects as the random effect. To investigate whether cognitive reserve influenced behavioral performance in the older adult group, a mixed effects model was conducted with fixed effects of load and cognitive reserve group, RT or Kc as the outcome variable and subject as the random effect. For neurophysiological data, alpha power and alpha frequency were the outcome variable, age, WM load, WM stage, and cognitive reserve (older adults only) were fixed effects and subjects as the random effect. Alpha power was log-transformed to normalize the data. Post-hoc pairwise t tests were performed in case

of significant main effects or interactions, with Bonferroni correction for multiple comparisons. Data were checked for normality using Shapiro–Wilk tests, and the residuals for the mixed effects models were examined via histograms and QQ plots. Associations between alpha power (calculated as a change from fixation) and task performance were performed using Spearman's correlation, as normality was violated in this case. In all tests, a p -value of less than .05 was considered statistically significant. Data were presented as mean \pm SD in text and mean \pm SEM in figures.

Cluster-based permutation tests were used to assess topographical differences in alpha power between age groups at each WM stage and load, between WM stages, and interactions between WM stage and age group at each load. Cluster-based permutations control for the type 1 error rate when comparing across multiple channels (Maris & Oostenveld, 2007). Clusters were defined as two or more neighboring electrodes for which the difference in alpha power between age groups (independent samples t test) or between WM stages (dependent samples t test) exceeded $p < .05$. Identified clusters were tested for significance using a permutation distribution, which was generated by combining alpha power values from both age groups/WM stages into a single set, randomly partitioning into two subsets, and taking the largest cluster-level statistic (i.e., the sum of t -values

within a cluster) from this random partition (Monte Carlo method; 2000 random permutations). If the cluster-level statistic observed from the original data was larger in absolute value than $> 95\%$ of random partitions, then, it was deemed significant ($p < .05$, two-tailed).

3 | RESULTS

3.1 | Behavioral results

While all participants performed the task successfully, task performance differed between memory load and age groups. A mixed effects linear model revealed significant main effects of age ($F_{1,52} = 47.5, p < .001$) and load ($F_{2,104} = 241.3, p < .001$) on RT, with a significant age by load interaction ($F_{2,104} = 17.8, p < .001$). Bonferroni corrected post-hoc tests revealed that younger adults responded significantly faster than older adults on load-1, load-3, and load-5 trials ($p < .001$ for all). Likewise, RT for load-5 trials was significantly slower than load-3 and load-1 trials, and load-3 was significantly slower than load-1 in both age groups ($p < .001$ for all) (Figure 2a).

To examine the interaction between age and load on RT, we examined the change in RT relative to load-1 between

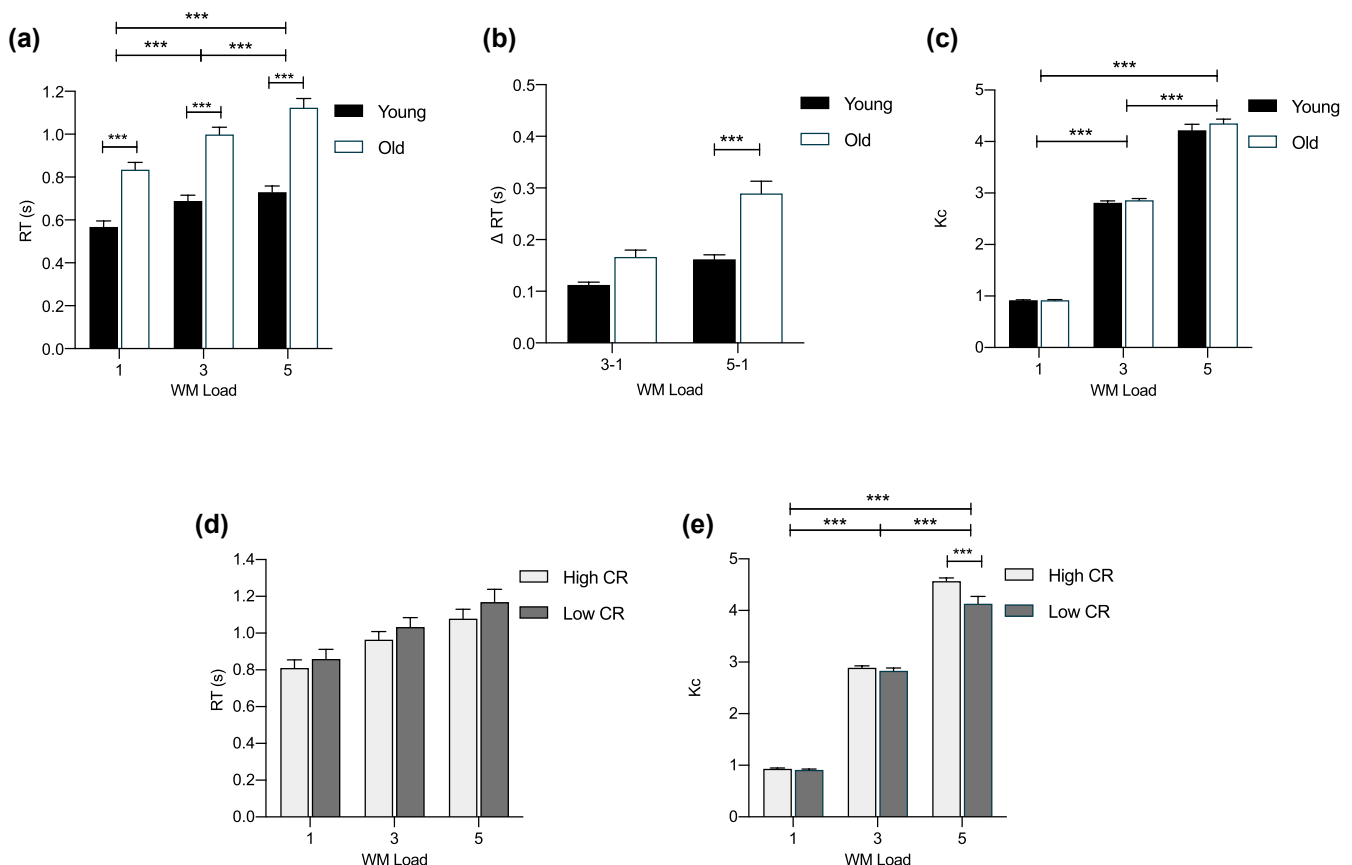


FIGURE 2 (a) RT for correct responses, (b) change in RT from load-1, and (c) Cowan's K for each WM load in younger and older adults. (d) RT for correct responses and (e) Cowan's K for older adults with high and low cognitive reserve. * $p < .05$, *** $p < .001$

age-groups. A mixed effects linear model revealed significant main effects of age ($F_{1,52} = 18.97, p < .001$) and load ($F_{2,52} = 94.96, p < .001$) on RT, with a significant age by load interaction ($F_{2,52} = 15.88, p < .001$). Bonferroni corrected post-hoc tests revealed that the increase in RT from load-1 to load-5 was larger in older adults compared to younger adults ($p < .001$). The increase in RT from load-1 to load-3 did not differ between age groups ($p = .16$) (Figure 2b). Likewise, a model investigating the effect of age and load on WM capacity revealed a main effect of load ($F_{2,104} = 1959, p < .001$). There was no significant main effect of age ($F_{1,52} = 1.03, p = .32$), nor a significant interaction between age and load ($F_{2,104} = 0.78, p = .46$) (Figure 2c).

A composite score of education years and NART results was used to calculate cognitive reserve in the older adults. The average score on the NART was 38.7 ± 5.25 , which corresponds to an average pre-morbid verbal IQ of 106.6 ± 6.8 . There was no significant difference in the age of the low and high cognitive reserve groups ($t_{28} = 0.27, p = .79$).

For RT, the model revealed a significant main effect of load ($F_{2,56} = 123.4, p < .01$), but no main effect of cognitive reserve ($F_{1,28} = 0.92, p = .34$), nor a load by cognitive reserve interaction ($F_{2,56} = 0.62, p = .54$) (Figure 2d).

For WM capacity, the model revealed a significant main effect of load ($F_{2,56} = 1604, p < .001$), a significant main effect of cognitive reserve ($F_{1,28} = 6.83, p = .014$) and a significant load by cognitive reserve interaction ($F_{2,56} = 4.58, p = .014$). Bonferroni corrected post-hoc tests revealed that on average, older adults with higher cognitive reserve had higher WM capacity than those with lower cognitive reserve ($p = .014$). Likewise, older adults with higher cognitive reserve had higher WM capacity in load-5 trials ($p < .001$). No significant differences in WM capacity were found between the high and low cognitive reserve group in load-3 ($p = .99$) or load-1 ($p = .99$) trials (Figure 2e).

Given that prior studies have demonstrated sex differences in verbal WM performance at high loads (Reed et al., 2017), we examined whether sex differences in RT and accuracy were present in our sample. A mixed effects linear model revealed no main effect of sex on RT ($F_{1,50} = 0.49, p = .48$), nor interactions between sex and age ($F_{1,50} = 0.11, p = .74$), sex and load ($F_{2,100} = 0.35, p = .70$), or age, sex, and load ($F_{2,100} = 3.1, p = .51$). Likewise, there was no main effect of sex on accuracy ($F_{1,50} = 1.2, p = .28$), nor interactions between sex and age ($F_{1,50} = 0.14, p = .71$), sex and load ($F_{2,100} = 1.6, p = .21$), or age, sex, and load ($F_{2,100} = 0.08, p = .92$).

3.2 | Alpha frequency and power modulation

Time frequency representation of power for young and older adults at each load are shown in Figure 3.

Participants in which an alpha peak was not detected at any WM stage or load were excluded from analysis of alpha peak frequency (4 older adults). A linear mixed effects model revealed significant main effects of age ($F_{1,48} = 4.7, p = .04$), WM stage ($F_{2,347} = 8.0, p < .001$) and load ($F_{2,347} = 5.8, p = .009$). There were no significant interactions. Bonferroni corrected post-hoc tests revealed that on average, older adults had lower alpha frequency than younger adults ($p = .04$) (Figure 3b). Alpha frequency was significantly higher in load-5 compared with load-1 trials ($p = .008$), but was not different between load-3 and load-5 trials or load-1 and load-3 trials (Figure 3c). Alpha frequency was significantly higher during encoding compared with fixation ($p = .006$) and retention ($p = .003$), but did not differ between retention and fixation (Figure 3d).

Alpha power was calculated using individual peak frequency at each WM stage (fixation, encoding, and retention) for each load. If a peak was not found in the retention period, the value for fixation was used to determine the frequency band for power calculations. If no peaks were found in any WM stage, the participant was excluded from further analysis (4 older adults). A mixed model revealed main effects of age ($F_{1,48} = 13.5, p < .001$), WM stage ($F_{2,384} = 240.4, p < .001$) and load ($F_{2,384} = 16.6, p < .001$), as well as an age x WM stage ($F_{2,384} = 3.6, p = .03$) and WM stage x load ($F_{4,384} = 7.1, p < .001$) interaction. Bonferroni corrected post-hoc tests revealed that overall, alpha power was significantly lower in older adults compared with younger adults ($p < .001$) (Figure 3b). Alpha power was significantly higher in load-1 trials compared with load-5 trials ($p < .001$), in load-3 trials compared with load-5 trials ($p < .001$), but not different between load-1 and load-3 trials (Figure 3c). Alpha power was significantly lower during encoding compared with both fixation ($p < .001$) and retention ($p < .001$), and alpha power during retention was significantly lower than in fixation ($p = .03$) (Figure 3d).

To examine the interaction between age and WM stage, mixed models were conducted separately in each age group with alpha power as the outcome variable, WM stage as the fixed effect and subject as the random effect. In older adults the model was significant ($F_{2,206} = 105.3, p < .001$), with Bonferroni corrected post-hoc tests revealing that for older adults, alpha power was significantly lower during encoding compared with fixation ($p < .001$) and retention ($p < .001$), and that alpha power during retention was significantly lower than during fixation ($p = .003$). The model was also significant in younger adults ($F_{2,190} = 108.8, p < .001$), with Bonferroni corrected post-hoc tests revealing that for younger adults, alpha power during encoding was lower compared with both fixation ($p < .001$) and retention ($p < .001$), but there was no difference between fixation and retention (Figure 4a). However, an independent samples *t* test revealed that the change in alpha power from fixation to retention was

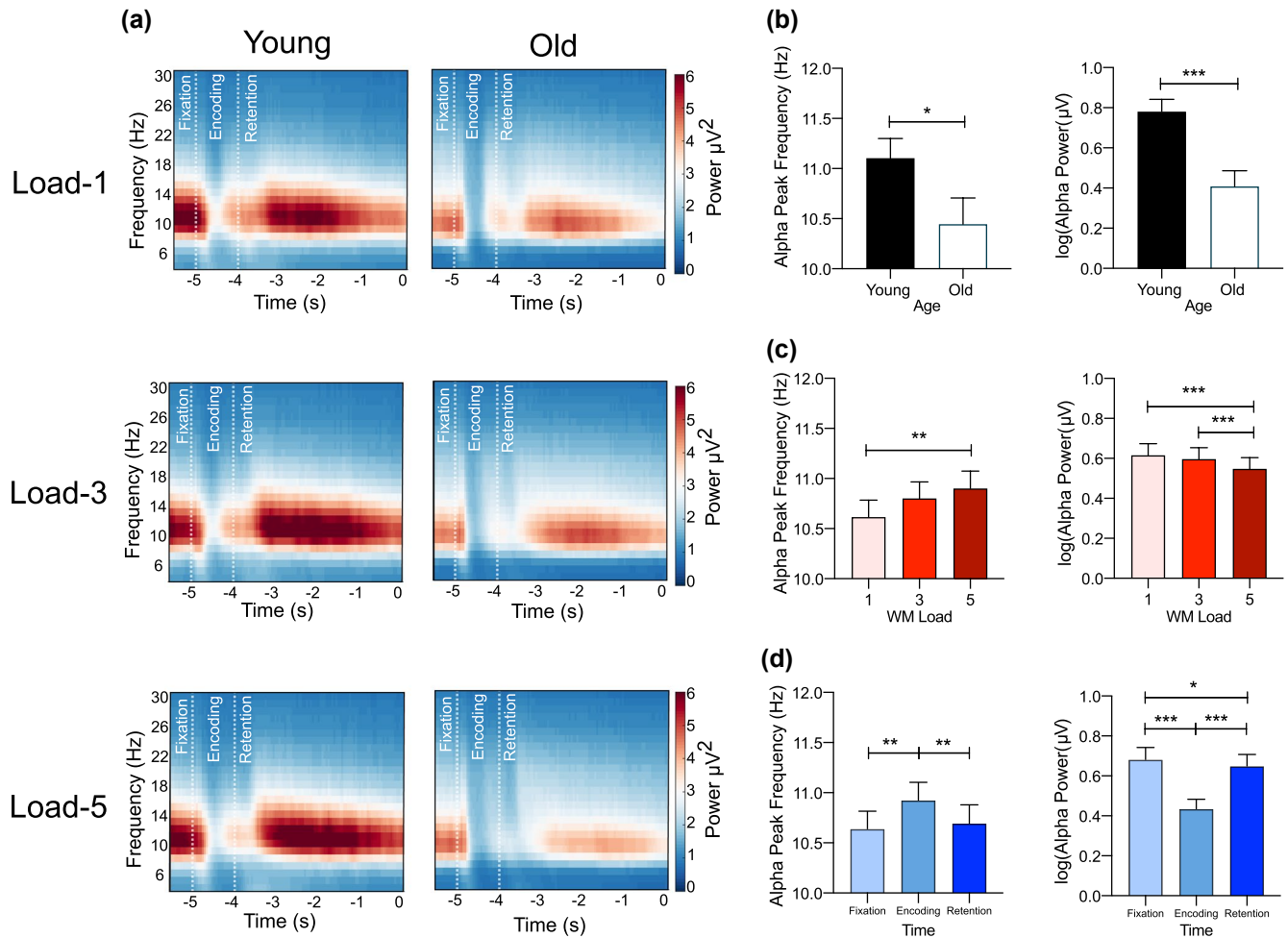


FIGURE 3 (a) Raw time frequency representations of power for each WM load and age group (b-d). Peak alpha frequency (left) and alpha power (right) between (b) age groups, (c) WM load and (d) stages of the WM task. * $p < .05$, ** $p < .01$, *** $p < .001$

not significantly different between age groups ($t_{42} = -1.4$, $p = .17$).

To investigate the interaction between WM stage and load, a mixed model was conducted for each WM stage, with load as the fixed effect and subjects as the random effect. For alpha power during the fixation period, the model was significant ($F_{2,98} = 3.4$, $p = .004$), though Bonferroni corrected post-hoc tests revealed no differences in alpha power between loads. For alpha power during encoding, the model was significant ($F_{2,98} = 66.3$, $p < .001$). Bonferroni corrected post-hoc tests revealed that during encoding, alpha power decreased with increasing memory load (all comparisons $p < .001$). For alpha power during retention, the model was significant ($F_{2,98} = 11.7$, $p < .001$). Bonferroni corrected post-hoc tests revealed that during retention, alpha power was significantly lower in load-5 trials compared with both load-1 ($p = .002$) and load-3 trials ($p < .001$), but did not differ between load-1 and load-3 trials (Figure 4b).

When examining the effect of cognitive reserve group on alpha activity in older adults, the model for alpha frequency revealed no significant main of WM stage ($F_{2,157} = 1.71$,

$p = .18$), cognitive reserve group ($F_{1,24} = 2.07$, $p = .16$) or load ($F_{2,15} = 2.36$, $p = .097$), and no significant interactions. For alpha power, the model revealed main effects of WM stage ($F_{2,192} = 118.6$, $p < .001$), load ($F_{2,192} = 10.7$, $p < .001$), and a WM stage by load interaction ($F_{4,192} = 3.75$, $p = .006$), but no main effects or interactions involving cognitive reserve ($p \geq .41$ for all).

3.3 | Retention period time course

For closer inspection of the temporal changes during the retention period, we calculated alpha power and peak frequency for each 0.5 s segment of the retention period. Only participants who had an alpha peak at each time point during the retention period were included in this analysis (19 older adults, 23 younger adults).

A mixed model with peak alpha frequency as the outcome, age, load, and time as fixed effects, and subjects as the random effect revealed main effects of time ($F_{7,982} = 20.2$, $p < .001$) and load ($F_{2,982} = 23.0$, $p < .001$). There were no

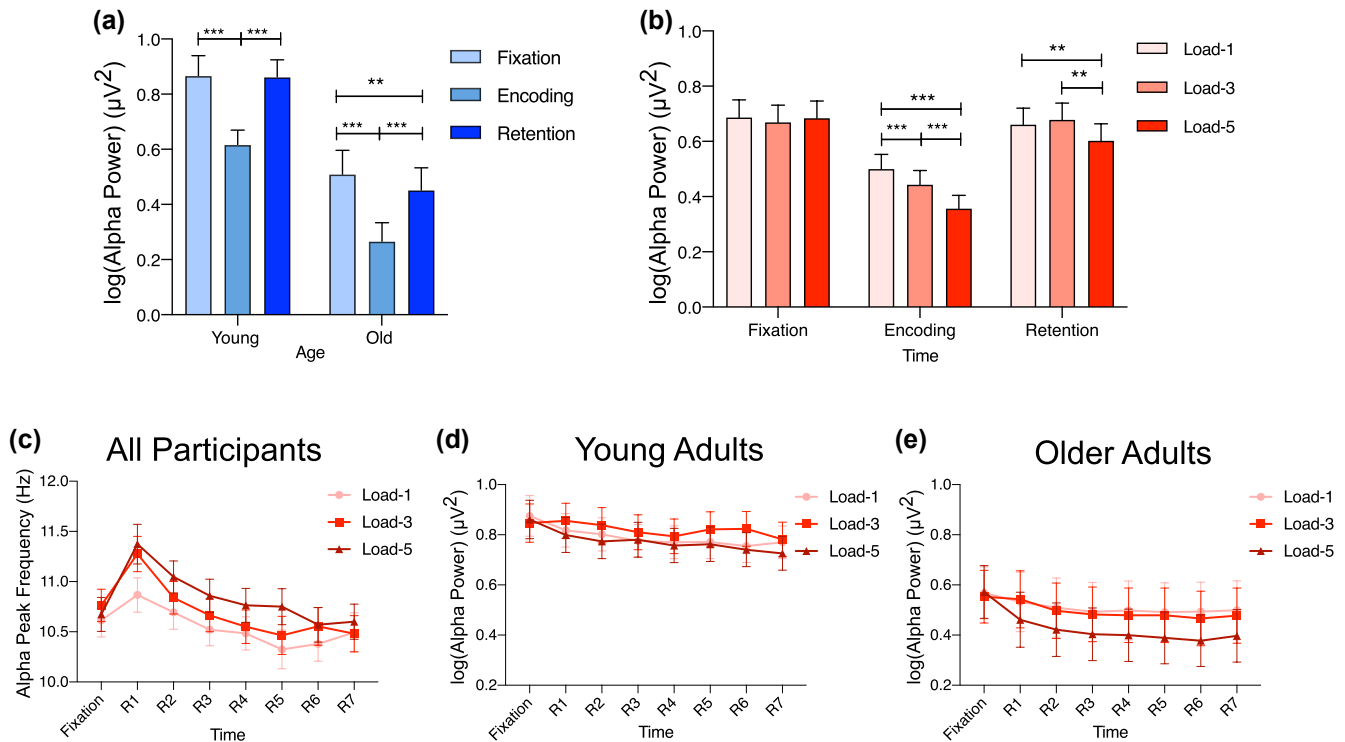


FIGURE 4 Alpha power modulation during the stages of the WM task between age groups (a) and WM loads (b). (c) Alpha peak frequency modulation across time and load during fixation and retention for all participants. (d-e) Alpha power modulation across time and load during fixation and retention for (d) young and (e) older adults. * $p < .05$, ** $p < .01$, *** $p < .001$

		Encoding				Retention			
		Young		Old		Young		Old	
		RT	Kc	RT	Kc	RT	Kc	RT	Kc
Load-1	ρ	−0.17	0.15	0.10	−0.09	−0.16	0.01	0.02	−0.17
	p	.43	.48	.62	.45	.45	.98	.94	.42
Load-3	ρ	−0.21	0.24	−0.09	−0.20	−0.20	−0.12	0.01	−0.09
	p	.33	.26	.68	.34	.34	.59	.97	.67
Load-5	ρ	−0.28	0.13	−0.06	−0.22	−0.22	−0.23	−0.02	0.02
	p	.18	.54	.75	.31	.29	.29	.92	.93

TABLE 1 Coefficients for correlations between RT and WM capacity (Kc), and alpha power during encoding and retention, relative to fixation, at each WM load for younger and older adults

other significant main effects or interactions. Bonferroni corrected post-hoc tests revealed that in R1 (i.e., 0.5–1 s from the start of the retention period), alpha frequency was higher than in all subsequent time increments (all $p < .001$). Likewise, alpha frequency was higher in load-5 during retention when compared with load-1 ($p < .001$) and load-3 ($p < .001$) (Figure 4c).

A mixed model with alpha power as the outcome, age, load, and time as fixed effects, and subjects as the random effect, revealed main effects of age ($F_{1,440} = 109.4$, $p = .025$), time ($F_{3,440} = 16.7$, $p < .001$), and load ($F_{2,440} = 15.5$, $p < .001$). There were no significant interactions. Bonferroni corrected post-hoc tests revealed that older adults had lower alpha power during fixation and retention than younger adults ($p =$

.007) (Figure 4d,e). Alpha power was significantly greater in the fixation period compared with each time point except R1. Further, alpha power was lower in load-5 trials compared with load-1 ($p < .001$) and load-3 ($p < .001$), but there were no differences between load-1 and load-3 (Figure 4d,e).

3.4 | Relationship between alpha power and frequency on task performance

Spearman correlation analyses revealed no significant association between alpha power during the encoding or retention period (relative to fixation) and RT or WM capacity for all WM loads in both age groups (Table 1). Likewise, there was

no significant relationship between alpha frequency and RT at each load for younger ($p > .23$ for all) and older ($p > .22$ for all) adults.

To further examine whether alpha frequency and power influenced WM performance, we sorted trials within each subject to a high or low RT group according to a median. Alpha frequency and power were then averaged over each RT group for each load during the encoding and retention periods. A mixed model with alpha frequency as the outcome, age, load, WM stage, and RT group as fixed effects and subject as the random effect revealed a main effect of age ($F_{1,50} = 12.37, p < .001$), but no main effects or interactions involving RT group ($p \geq .09$ for all). Likewise, a mixed model with alpha power as the outcome revealed main effects of WM stage ($F_{1,572} = 646.2, p < .001$), age ($F_{1,52} = 13.77, p < .005$), and load ($F_{2,572} = 26.26, p < .001$), but no main effects or interactions involving RT group ($p \geq .08$ for all).

3.5 | Scalp distribution of alpha power

In order to rule out the effect of topographical shifts in our data and determine whether electrodes other than those in the parieto-occipital/occipital region showed similar patterns of alpha activity during the task, we investigated whether the spatial distribution of alpha power (averaged over individualized alpha bands) differed between age groups at each WM stage and load. Likewise, given that our task involved verbal, rather than visual WM, to determine whether the pattern of alpha power changes we observed during the task were similar in non-posterior electrodes, we compared 500 ms of the encoding and retention periods (R4 time point) with fixation, within each age group.

After averaging the alpha frequency band (± 2 Hz peak alpha frequency), cluster-based permutation tests revealed

no significant differences in the spatial distribution of alpha power between age groups at any WM stage or load (no significant clusters) (Figure 5). Therefore, we did not find evidence to suggest that the raw alpha power scalp distributions differ across age groups.

In both age groups, cluster-based permutation tests revealed a significant decrease in alpha power in encoding from fixation in load-1, load-3, and load-5 trials (all comparisons $p < .001$). Conversely, significant increases in alpha power in retention from fixation were seen in load-3 for both younger ($p = .03$) and older ($p = .04$) adults, which were most pronounced over the right parietal, parieto-occipital, and occipital electrodes. No significant differences between fixation and retention were seen in load-1 in younger ($p = .08$) or older ($p = .10$) adults. While no significant differences between fixation and retention were seen in load-5 for young adults, there was a significant decrease in alpha power from fixation in older adults ($p = .03$), most pronounced in the left centro-parietal, central, and fronto-central electrodes. However, changes in alpha power between WM stages did not differ between age groups at any load (no significant clusters) (Figure 6).

4 | DISCUSSION

In this study, we investigated age-related differences in visual alpha power and frequency during the encoding and retention stages of WM in response to varying loads. Behaviorally, older adults were slower to respond at all WM loads compared to younger adults, but there were no age differences in WM capacity. However, older adults with higher cognitive reserve performed better on load-5 trials compared with those with lower cognitive reserve. Overall, both alpha frequency and power were lower in older adults than in younger adults

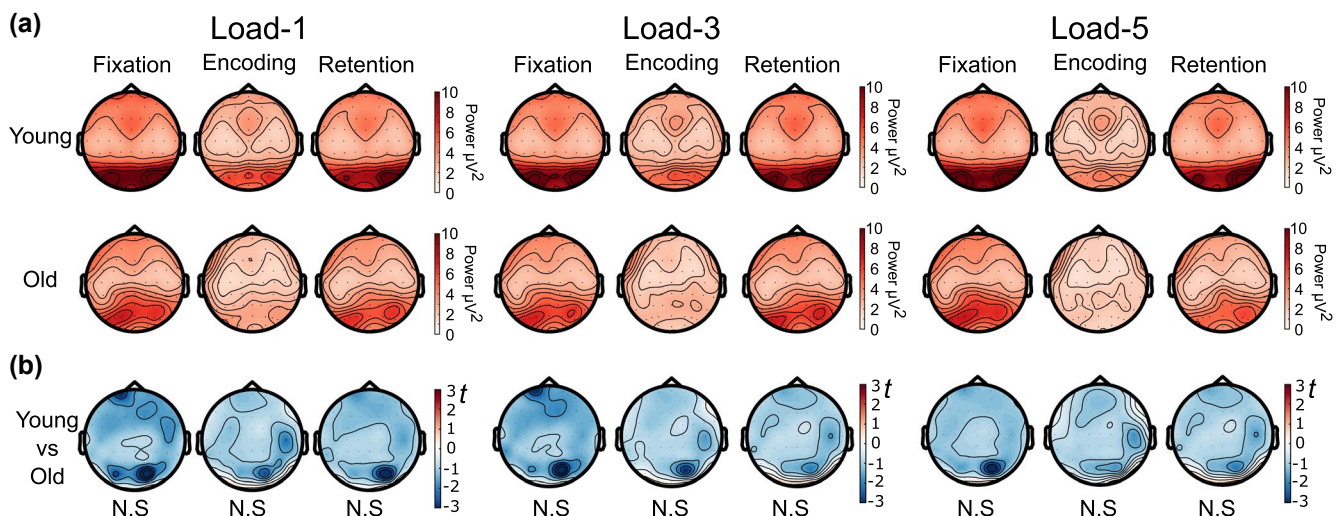


FIGURE 5 (a) Topographical representation of raw power for young and older adults at each WM load and stage. (b) t -statistics for cluster-based permutation tests for age comparisons at each WM stage and load

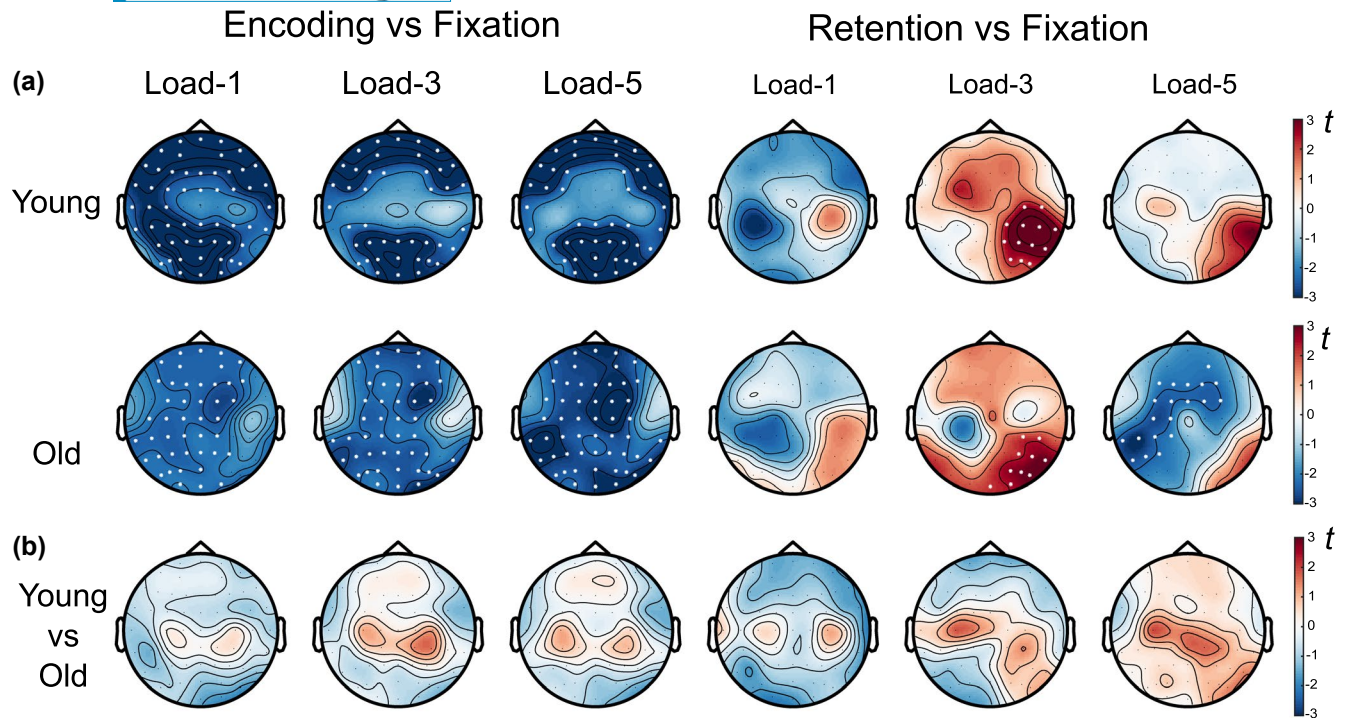


FIGURE 6 (a) t -statistics for cluster-based permutation tests for encoding and retention compared with fixation at each WM load and each age group. (b) t -statistics for cluster-based permutation tests for an interaction effect between age groups and the difference between encoding and retention from fixation, at each WM load

in each WM stage. During encoding, alpha power decreased with increasing WM load and alpha frequency increased. Regardless of age, alpha power was lower in load-5 than in load-1 and load-3 trials, but alpha frequency increased with load during retention. While alpha power during retention was lower than fixation in older, but not younger adults, the relative change from fixation was not significantly different between age groups. Further, individual differences in visual alpha power did not predict individual task performance within age groups, at any WM loads.

4.1 | At all WM loads, older adults are slower to respond to the probe than younger adults, but WM capacity does not differ across age groups

As expected, older adults were slower to respond to the probe at all WM loads compared with younger adults. However, we found no age differences in WM capacity, with many participants from both age groups performing at near ceiling level. Therefore, the difference in RT in the older group likely does not reflect WM deficits, but rather age-related changes in processing speed (Salthouse, 1996). It has been shown that verbal WM might be more resistant to age effects than visual WM (Hale et al., 2011), and it is possible that our task was not difficult enough to capture age-differences. Taken together, we did not find strong evidence for working memory

impairment with aging in our sample, although this may be specific to the type of task performed.

4.2 | Alpha power is modulated by load during the encoding and retention period for both younger and older adults

Alpha suppression occurred during the encoding period in both age groups, with a strengthening of this response with increasing WM load. Alpha suppression has long been thought to reflect attentional processes (Klimesch, 1997), as when attention is directed to external visual events, alpha power in visual cortex decreases with increasing attention demands (Rajagovindan & Ding, 2010; Sauseng et al., 2005). Therefore, a decrease in alpha power during encoding likely reflects an increase in cortical excitability to enhance stimulus processing (Heinrichs-Graham & Wilson, 2015; Klimesch, 1997; Murphy et al., 2019; Romei et al., 2010; Thut et al., 2011). Although alpha power was lower in older relative to younger adults, our results suggest that alpha suppression during encoding follows a similar pattern across age groups. This is consistent with previous studies that have shown that suppression processes during the encoding period, as indicated by alpha activity, remain relatively intact in older adults (Gazzaley et al., 2008). However, even though both age groups demonstrated poorer performance with increasing WM load, individual differences in alpha

suppression during encoding did not support WM performance under varying loads in our task.

In both age groups, we found that alpha power decreased under higher WM loads during the retention period. This contrasts with the previously reported increase in visual alpha power during retention in younger adults completing modified Sternberg tasks (Jensen et al., 2002; Proskovec et al., 2019; Tuladhar et al., 2007; Wang et al., 2016). Though an increase in alpha power during retention has been interpreted to reflect inhibition of task irrelevant information, in lateralized tasks, alpha power decreases in task-relevant brain regions, but increases in task-irrelevant regions, and the magnitude of this reduction correlates with WM load (Sauseng et al., 2009). Likewise, in a study employing a delayed match-to-sample task, stronger alpha suppression during the retention period was seen under higher visual WM loads, which was interpreted to reflect increased activation of visual cortex to maintain the neural representation of remembered items (Fukuda et al., 2015). It is possible that the decrease in alpha power during retention for load-5 trials in the current study reflects specific features of the task and the strategies used by participants. Whereas encoding stimuli are presented sequentially in the classical Sternberg paradigm (Sternberg, 1966), our encoding stimuli were presented simultaneously, similar to the approach taken in visual WM delay match-to-sample tasks. Therefore, it is possible participants were using a visual strategy to retain the information in higher loads, leading to decreases in alpha power.

In terms of age-related findings, our results contrast with a recent study employing a 6-letter modified Sternberg task, where it was observed that older adults exhibited a greater increase in visual alpha power during the retention period compared to younger adults (Proskovec et al., 2016). This was interpreted in that study to align with the Compensation-Related Utilization of Neural Circuits Hypothesis (CRUNCH) (Reuter-Lorenz & Cappell, 2008), which suggests that generally, people recruit more brain regions when task-difficulty increases. Older adults are thought to recruit more cortical regions at lower loads than younger adults to compensate for cognitive decline. In our study, however, while younger adults demonstrated no difference in alpha power during the retention period compared with fixation, older adults demonstrated a decrease in power from fixation, regardless of load. While this difference in alpha power relative to fixation was not significantly different between age groups, if alpha suppression is indicative of the active maintenance of WM representations, the decrease in alpha power seen at load-5 in older adults may be another form of compensatory neural strategy.

Along with the characteristic decrease in alpha power and frequency, previous research has also shown a posterior to anterior shift in the topographic distribution of alpha with age (McEvoy et al., 2001). While we did not find evidence for age differences in the spatial distribution of alpha power

during the task, we found that in the retention period of load-5 trials, older adults demonstrated a decrease in alpha power in left centro-parietal, central, and fronto-central electrodes. It is possible that this decrease in alpha power may reflect engagement of brain regions involved in verbal processing (Rottschy et al., 2012), or potentially another form of compensatory strategy for older adults at higher WM loads. However, there was no interaction between age group and the difference in alpha power between fixation and retention in load-5. As such, clarifying the role of alpha suppression during verbal WM and cognitive aging is a topic for future research.

Further, studies investigating the alpha rhythm in both younger and older adults tend to define alpha as a narrow band (usually 8–12 Hz) and average over spectral activity in that range for all subjects. Given that peak alpha frequency decreases with age, alpha power may fall outside of the fixed alpha frequency band, or activity in theta/beta frequencies may be included in the alpha window. Our results show that when alpha power is calculated based upon individual peak alpha frequency, the pattern of alpha activity across WM stages in older adults appears similar to that of younger adults but lower in magnitude, even when WM performance is matched to that of younger adults.

4.3 | Age, task, and load modulation of alpha frequency

Age has long been known as one of the most important factors influencing the frequency of the alpha rhythm (Klimesch, 1997). Resting state alpha peak frequency has been shown to be a stable neurophysiological trait in healthy younger and older adults (Grandy et al., 2013), however, it is becoming increasingly clear that alpha peak frequency shifts during cognitive tasks. In particular, a study employing an n-back task demonstrated a load-dependent increase in alpha frequency in healthy young adults (Haegens et al., 2014), while in a modified Sternberg task, a load-dependent decrease in alpha frequency during encoding and an increase during retention were apparent (Babu Henry Samuel et al., 2018).

One hypothesis that may explain the changes in peak alpha frequency during WM postulates that alpha frequency is a manifestation of an “internal clock” which controls the brain’s speed of information processing (Klimesch et al., 1996). According to this theory, the higher the alpha frequency, the faster the cognitive processing, for example, during WM performance. In line with this, alpha frequency should increase with load during encoding to meet the sensory demands of encoding more information, and decrease with load during retention to reduce the rate of sensory processing, as slower alpha frequency may allow for longer windows of suppression (Jensen & Mazaheri, 2010; Sadaghiani & Kleinschmidt, 2016), and therefore, facilitate

protection against interference during WM. Our results partially support this idea. We found an increase in alpha frequency during encoding, but while there was a decrease in alpha frequency in retention from encoding, we did not find evidence for a decrease from fixation. Likewise, while we did observe an overall decrease in alpha frequency as the retention period progressed, it was highest in load-5 trials. According to the internal clock theory, higher alpha frequency during retention should be counterproductive to performance, as presumably this reflects less inhibition to protect the WM store. The proposed deleterious role of high alpha frequencies was shown in a recent study which demonstrated that higher peak frequency during retention led to slower RT (Babu Henry Samuel et al., 2018). The link between alpha frequency and processing speed, however, depends on alpha power representing an inhibitory mechanism during retention- an idea which is inconsistent with the findings of this study. Therefore, determining the task-relevance of alpha peak frequency during WM is a topic for future research.

4.4 | Cognitive reserve

Within the older adult group, we found that participants with higher composite cognitive reserve had a higher WM capacity at load-5, but not at load-3 and load-1, than those with low cognitive reserve. A previous study employing a verbal WM Sternberg task that increased in load from 1 to 7 reported similar results, with subjects with higher cognitive reserve performing more accurately in the task at higher loads than those with lower cognitive reserve (Spear & Soldan, 2015). However, within the older adult group, we did not see differences in alpha power or frequency during the task between cognitive reserve groups. Theoretically, it is proposed that cognitive reserve does not directly alter age-related neural changes, but rather modifies the behavioral outcome of these anatomical or physiological changes (Barulli & Stern, 2013). Our findings align with this interpretation, given that alpha frequency and power decreased with age at all loads, but the high cognitive reserve group were able to perform better at higher loads compared with the low cognitive reserve group. However, cognitive reserve may influence other oscillatory dynamics at rest and during task performance that were not investigated in this study, presenting an avenue for further investigation.

4.5 | Limitations

There are several limitations of this study. First, the age range of the older adult sample is much larger (36 years) than the younger adult sample (17 years). Given that trajectories of change in cognitive performance are largely heterogeneous across older adults (Hayden et al., 2011), future work should take into account individual differences in age-related WM

decline. Second, though the modified Sternberg task used in this study allowed the temporal delineation of the encoding and retention stages of WM, this task does not assess the manipulation of items in WM (Baddeley, 1992). Further research is required to expand upon whether alpha activity is altered with age during the manipulation component of WM processing. Third, when WM accuracy is high, values of K may underestimate WM capacity (Rouder et al., 2011). As participants in both age groups performed at a ceiling level, our task may not have been difficult enough to capture true WM capacity. Fourth, due to technical reasons, we were not able to collect clean data from the mastoids and opted to use average reference instead. We recognize that this may be a limitation when comparing our results to others in the literature. Finally, lower alpha power seen with age might be due to structural brain differences such as atrophy in cortical tissue seen with age, brain size or skull thickness which are not able to be accounted for or assessed with EEG (Frodal et al., 2001). Future work may investigate how structural brain changes influence oscillatory activity recorded during WM task performance.

5 | CONCLUSION

Our results suggest that alpha power and frequency were reduced with advanced age; however, both frequency and power were modulated in a similar task- and load-dependent manner during WM in both younger and older adults. Additionally, these age-related changes in alpha do not differ based on an individual's composite cognitive reserve, even when WM performance differs across cognitive reserve groups. Future research should elaborate the functional significance of alpha power and frequency changes that accompany WM performance in cognitive aging.

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CONFLICTS OF INTEREST

The authors confirm that there are no known conflicts of interest associated with this publication.

AUTHOR CONTRIBUTION

Conceptualization; Formal analysis; Investigation; Methodology; Project administration; Software; Visualization; Writing-original draft; Writing-review & editing: Sghirripa
Investigation; Software; Writing-review & editing: Graetz

Investigation; Writing-review & editing: Merkin
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