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

Corresponding author: Sabrina Sghirripa [a, b, c]
sabrina.sghirripa@adelaide.edu.au

Lynton Graetz [a, c]
lynton.graetz@adelaide.edu.au

Ashley Merkin [a, c]
ashley.merkin@adelaide.edu.au

Nigel C Rogasch [c, d, e]
nigel.rogasch@adelaide.edu.au

John G Semmler [b]
john.semmler@adelaide.edu.au

Mitchell R Goldsworthy [a, b, c, d]
mitchell.goldsworthy@adelaide.edu.au

[a] Neuromotor Plasticity and Development, Adelaide Medical School, The University of Adelaide, Adelaide, Australia
[b] Discipline of Physiology, Adelaide Medical School, The University of Adelaide, Adelaide, South Australia, Australia
[c] South Australian Health and Medical Research Institute, Adelaide, South Australia, Australia
[d] Discipline of Psychiatry, Adelaide Medical School, The University of Adelaide, Adelaide, South Australia, Australia
[e] Brain, Mind and Society Research Hub, School of Psychological Sciences, Turner Institute for Brain and Mental Health and Monash Biomedical Imaging, Monash University, Melbourne, Australia

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 and 30 older adults performed a modified Sternberg task with varying load conditions. 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. However, individual differences in alpha power did not predict performance within age groups or WM loads. We demonstrate that between age groups, alpha power and frequency are modulated in a similar task- and load-dependent manner during WM processes, but age-related changes in alpha are not associated with poorer WM performance in older adults.

Key words: EEG, cognitive ageing, working memory, alpha oscillations

1 Introduction

Working memory (WM) is the ability to actively maintain and/or manipulate information to guide immediate cognitive processing (Baddeley, 1992), and is particularly vulnerable to age-related decline. Compared to younger adults, healthy older adults are able to store fewer items in WM, less able to manipulate those items (Fisk and Warr, 1996), and 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 load-related neural mechanisms underlying such age differences are not well understood.

Advancing age is associated with progressive changes in the frequency and power of neural oscillations (Klass and Brenner, 1995; Klimesch, 1999). Alpha (~8-12Hz) is perhaps the most affected frequency band in ageing, 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 phases: 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 phase, 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 visual alpha increases during retention, particularly under higher 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 and Mazaheri, 2010). In lateralised WM tasks where subjects attend and memorise the information to 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 phase, likely reflecting attentional processes (Heinrichs-Graham and 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).

However, as the aforementioned studies involved only younger adults, it is unclear whether visual alpha activity contributes to 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 load-dependent WM performance. Likewise, while previous studies have found evidence for task- and load-related alpha frequency modulation, 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 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 phases. 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.

2 Method

2.1 Participants

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=0.857). 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.

2.2 Working memory task

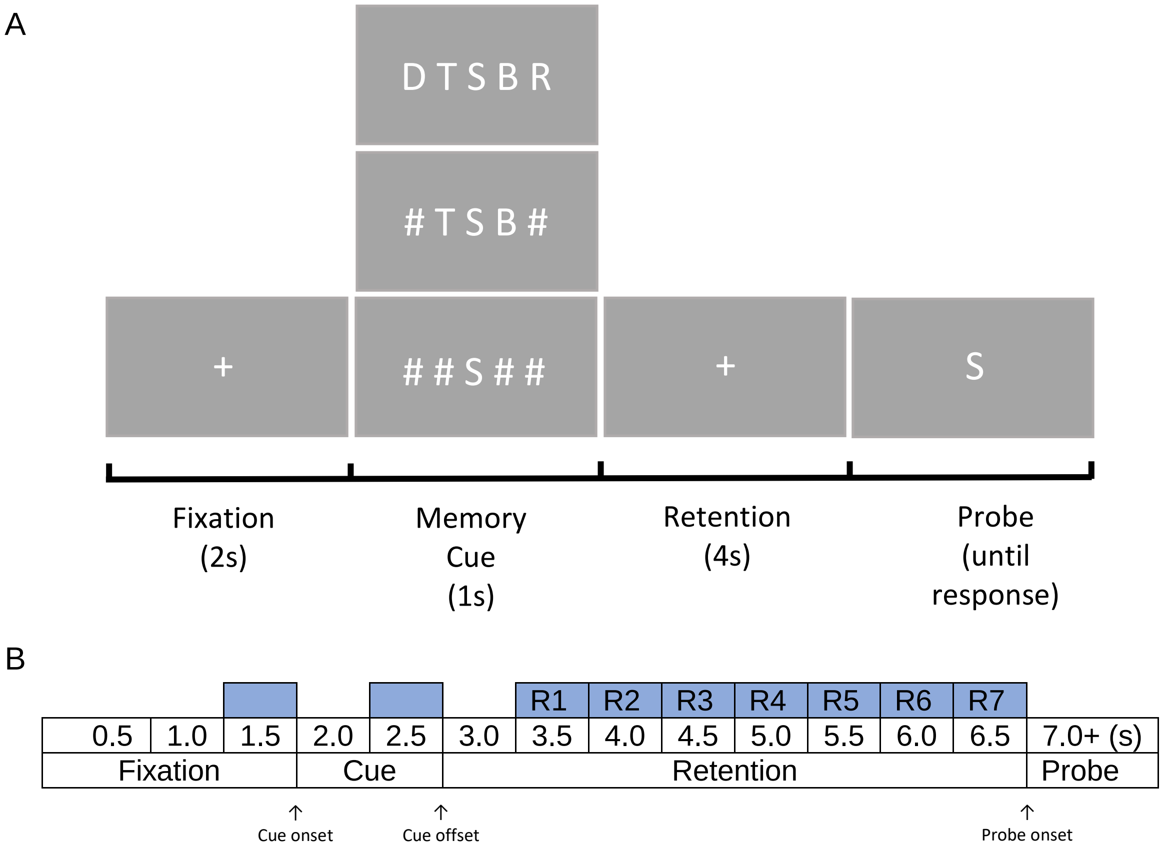

Figure 1. (A) Modified Sternberg WM task. Each trial contained four phases: 1) fixation lasting for 2 s, 2) encoding, where a 1, 3 or 5 load memory set was displayed for 1 s, 3) a 4 s retention phase and 4) a retrieval phase where the subject responded to whether the probe was part of the memory set. (B) Schematic for EEG analysis periods for fixation, encoding (cue) and retention.

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 centre 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 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 familiarise 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.

To quantify WM performance, both accuracy (% correct) and reaction time (RT) for correct trials were calculated for each load condition.

2.3 EEG Data Acquisition

EEG data were recorded from 62 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). Conductive gel was inserted into each electrode using a blunt-needle syringe in order to reduce impedance to <5 kΩ. The ground electrode was located at AFz. Signals were amplified 20x, online filtered (DC-553 Hz), sampled at 2048 Hz and 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 and Makeig, 2004) and custom scripts using MATLAB (R2018b, The Mathworks, USA). For task data, each block of EEG data was merged and incorrect trials, as well as trials with outlier RT (defined as >3xSD) were removed. Bad and unused channels were then removed. The data were then band-pass (1-100 Hz) and band-stop (48-52 Hz) filtered, down-sampled to 256 Hz and epoched -6s to 1s relative to the beginning of the probe. Independent component analysis (ICA) was then conducted using the FastICA algorithm (Hyvärinen and Oja, 2000) to remove artefacts resulting from eye-blinks and persistent scalp muscle activity. Data were then checked for remaining artefact via visual inspection and trials were removed if necessary. Remaining trials were then split according to the memory load condition.

2.5 Spectral Analysis

FieldTrip toolbox (Oostenveld et al., 2011) was used to analyse 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 3 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 cue (figure 1B) (Babu Henry Samuel et al., 2018; Wang and 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 phase of the task (fixation, encoding, retention) and for each load. Alpha frequency range was defined as 2 Hz above and below the peak frequency between 6 to 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 time point (fixation, cue 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 analyse the behavioural and neurophysiological data. For behavioural data, performance (RT and accuracy) was the outcome variable, WM load and age were fixed effects and subjects as the random effect. For neurophysiological data, alpha power and alpha frequency were the outcome variable, age, WM load and time were fixed effects and subjects as the random effect. Alpha power was log-transformed to normalise the data. Post-hoc pairwise t-tests were performed in case of significant main effects or interactions, with Bonferroni correction for multiple comparisons. Associations between alpha power (calculated as a change from fixation) and task performance were performed using Spearman’s correlation. In all tests, a p-value of less than 0.05 was considered statistically significant. Data were presented as mean ± SD in text and mean ± SEM in figures.

3 Results

3.1 Behavioural 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<0.001) and load ($F_{2,104}$= 241.3, p<0.001), with a significant age by load interaction ($F_{2,104}$ = 17.8, p<0.001) on RT. Bonferroni corrected post-hoc tests revealed that younger adults responded significantly faster than older adults on load-1 (p<0.001), load-3 (p<0.001) and load-5 trials (p<0.001). Likewise, RT for load-5 trials was significantly slower than load-3 (p<0.001) and load-1 trials (p<0.001), and load-3 was significantly slower than load-1 in both age groups (p<0.001) (figure 2A).

The model revealed a significant main effect of load on accuracy ($F_{2,104}$= 19.7, p<0.001). There was no significant main effect of age ($F_{1,52}$ = 0.91, p = 0.34), nor a significant interaction between age and load ($F_{1,104}$= 0.4, p = 0.7). Post-hoc tests revealed that accuracy was significantly different between load-1 and load-5 trials (p<0.001) and load-3 and load-5 trials (p<0.001), but not between load-1 and load-3 trials for both age groups (p=0.542) (figure 2B).

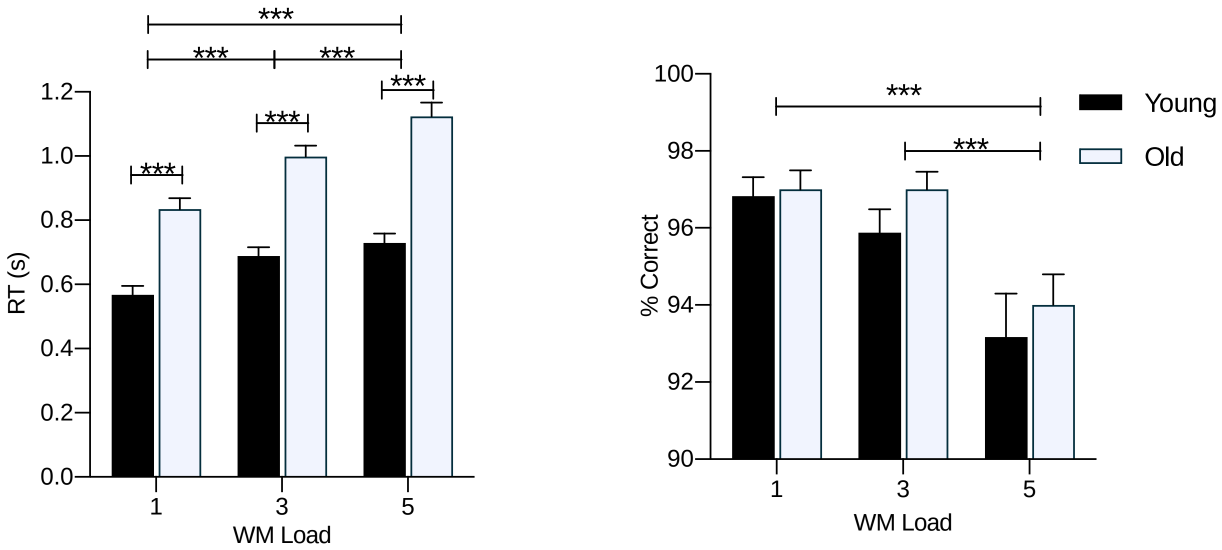

Figure 2. RT for correct responses (A) and percentage of correct responses (B) for each WM load in younger and older adults. ***p<0.001.

3.2 Peak Alpha Frequency

Participants in which an alpha peak was not detected at any time point or load were excluded from this analysis (4 older adults).

A linear mixed effects model revealed significant main effects of age ($F_{1,48}$ = 4.7, p = 0.04), time ($F_{2,347}$ = 8.0, p <0.001) and load ($F_{2,347}$ = 5.8, p = 0.009). There were no significant interactions.

Bonferroni corrected post-hoc tests revealed that on average, older adults had lower alpha frequency than younger adults (*p*=0.04) (figure 3A). Alpha frequency was significantly higher during the cue compared with fixation (p =0.006) and retention (p=0.003), but did not differ between retention and fixation (Figure 3B). Alpha frequency was significantly higher in load-5 compared with load-1 trials (*p*=0.008), but was not different between load-3 and load-5 trials or load-1 and load-3 trials (Figure 3C).

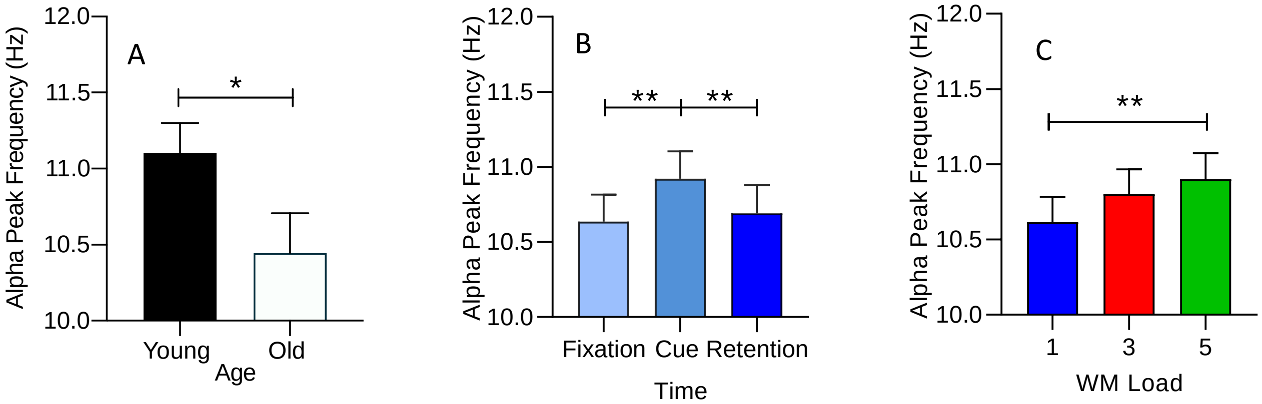

Figure 3. Peak alpha frequency between age groups (A), stages of WM task (B) and WM load (C). * *p* <0.05, ** *p* <0.01, *** *p*<0.001

3.3 Alpha Power

Alpha power was calculated using individual peak frequency at each time point (fixation, cue, 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 at any time point, the participant was excluded from further analysis (4 older adults).

A mixed model revealed main effects of age ($F_{1,48} = 13.5$, $p<0.001$), time ($F_{2,384} = 240.4$, $p<0.001$) and load ($F_{2,384} = 16.6$, $p<0.001$), as well as an age x time ($F_{2,384} = 3.6$, $p=0.03$) and time x load ($F_{4,384} = 7.1$, $p<0.001$) interaction.

Bonferroni corrected post-hoc tests revealed that overall, alpha power was significantly lower in older adults compared with younger adults (*p*<0.001) (figure 4A). Alpha power was significantly lower during the cue compared with both fixation (*p*<0.001) and retention (*p*<0.001), and alpha power during retention was significantly lower than in fixation (p=0.03) (figure 4B). Alpha power was significantly higher in load-1 trials compared with load-5 trials (p<0.001), in load-3 trials compared with load-5 trials (p<0.001), but not different between load-1 and load-3 trials (figure 4C).

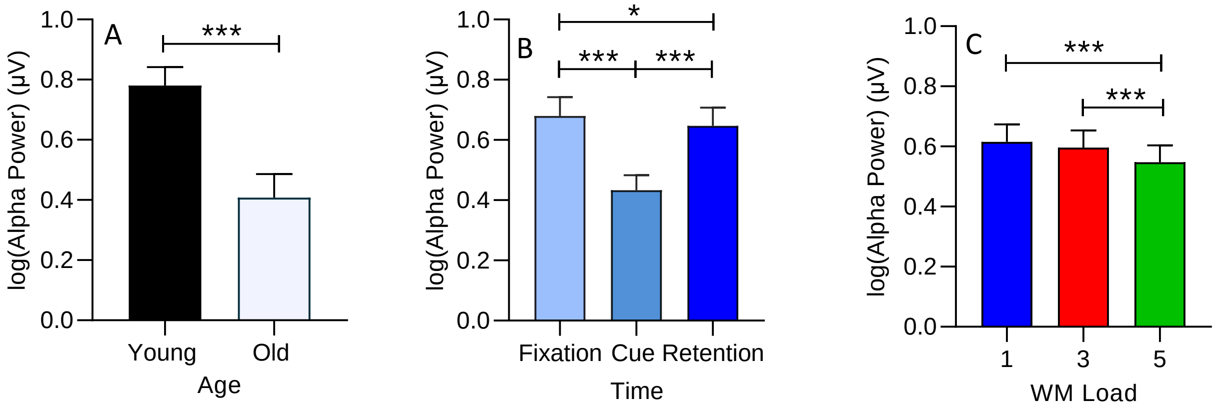

Figure 4. Alpha power between age groups (A), stages of WM task (B) and WM load (C). * *p* <0.05, *** *p*<0.001

To examine the interaction between age and time, mixed models were conducted separately in each age group with alpha power as the outcome variable, time as the fixed effect and subject as the random effect. In older adults the model was significant ($F_{2,206}$=105.3, p <0.001), with Bonferroni corrected post-hoc tests revealing that for older adults, alpha power was significantly lower during the cue compared with fixation (p<0.001) and retention (p<0.001), and that alpha power during retention was significantly lower than during fixation (p=0.003). The model was also significant in younger adults ($F_{2,190}$=108.8, p <0.001), with Bonferroni corrected post-hoc tests revealing that for younger adults, alpha power during the cue was lower compared with both fixation (p<0.001) and retention (p<0.001), but there was no difference between fixation and retention (figure 5A). However, an independent samples t-test revealed that the relative change in alpha power from fixation to retention was not significantly different between age groups (t_{42}=-1.4, *p*=0.17).

To investigate the interaction between time and load, a mixed model was conducted for each time period, 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* = 0.004), though Bonferroni corrected post-hoc tests revealed no differences in alpha power between loads. For alpha power during the cue, the model was significant ($F_{2,98}$ = 66.3, *p*<0.001). Bonferroni corrected post-hoc tests revealed that during the cue, alpha power decreased with increasing memory load (all comparisons p<0.001). For alpha power during retention, the model was significant ($F_{2,98}$ = 11.7, *p*<0.001). Bonferroni corrected post-hoc tests revealed that during retention, alpha power was significantly lower in load-5 trials compared with both load-1 (*p*=0.002) and load-3 trials (*p*<0.001), but did not differ between load-1 and load-3 trials (figure 5B).

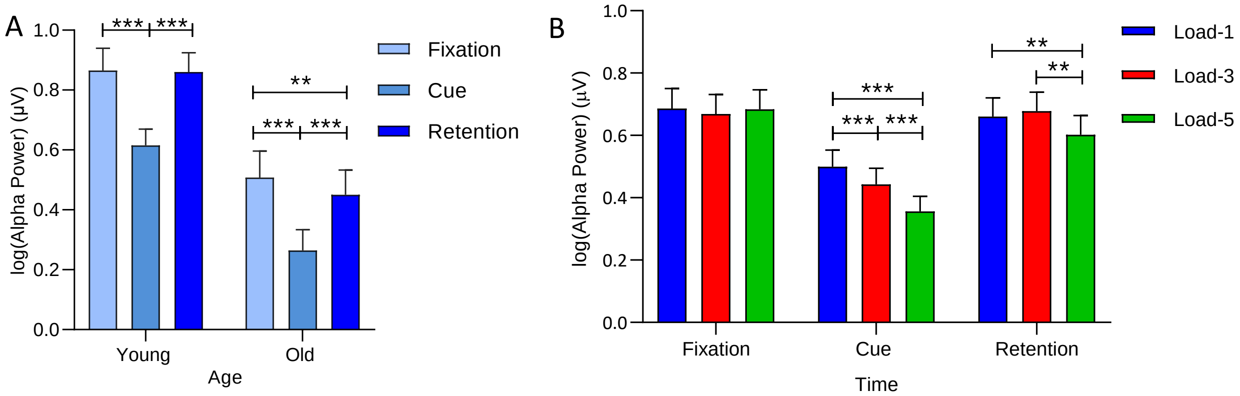

Figure 5. Alpha power modulation during the phases of the WM task between age groups (A) and WM loads (B) * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

3.4 Retention period time course

For closer inspection of the temporal changes during the retention period, we calculated alpha power and peak frequency for each 0.5s 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 ($F_{7,982} = 20.2$, $p<0.001$) and load ($F_{2,982} = 23.0$, $p<0.001$). There were no other significant main effects or interactions. Bonferroni corrected post-hoc tests revealed that in R1 (i.e. 0.5-1s from the start of the retention period), alpha frequency was higher than in all subsequent time increments (all $p<0.001$). Likewise, alpha frequency was higher in load-5 during retention when compared with load-1 ($p<0.001$) and load-3 ($p<0.001$) (figure 6A).

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 ($F_{1,440} = 109.4$, $p=0.025$), time ($F_{3,440} = 16.7$, $p<0.001$) and load ($F_{2,440} = 15.5$, $p<0.001$). 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 ($p=0.007$). 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 ($p<0.001$) and load-3 ($p<0.001$), but there were no differences between load-1 and load-3 (figure 6B).

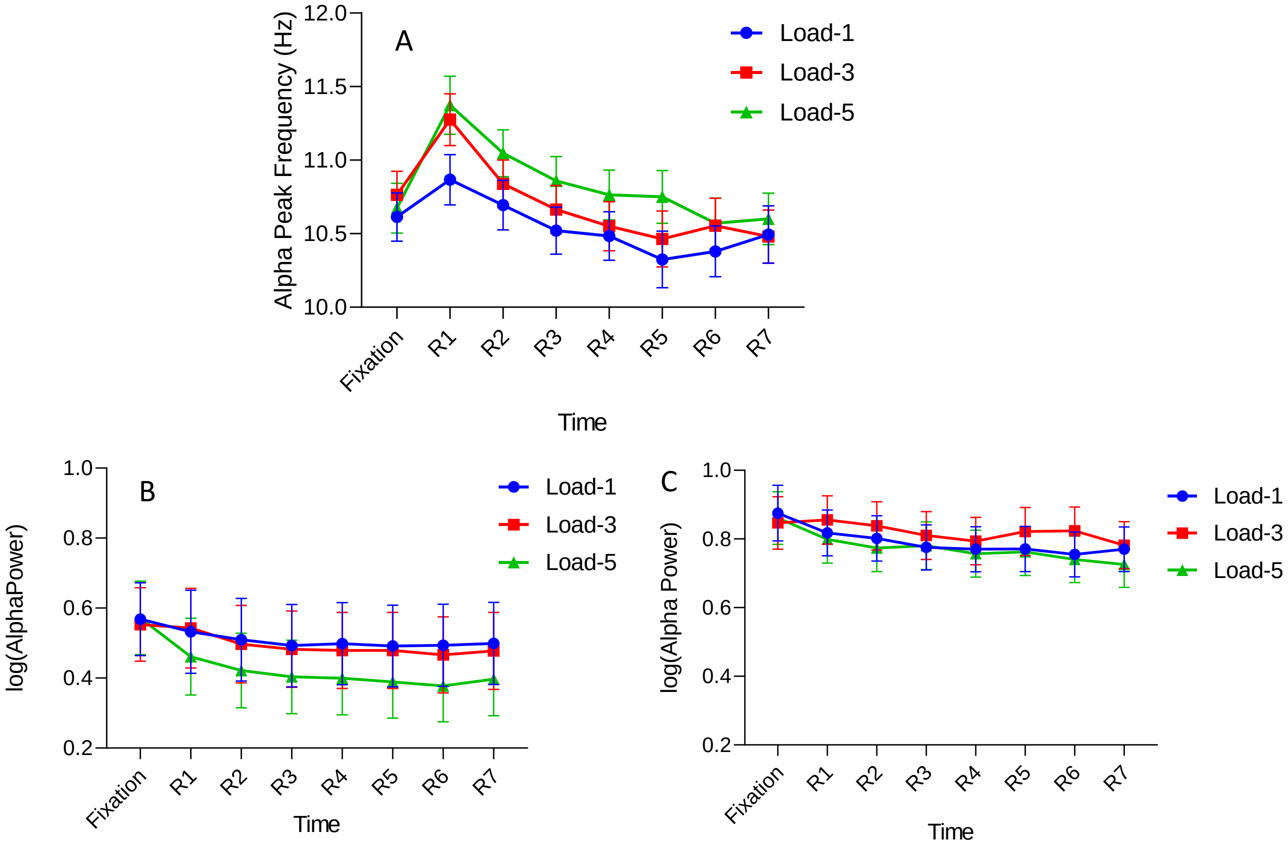

Figure 6. Alpha peak frequency modulation across time and load (A) and alpha power modulation across time and load during fixation and the retention period for younger (B) and older (C) adults.

3.5 Effect of alpha power on performance

Spearman correlation analyses revealed no significant association between alpha power during the encoding or retention period (relative to fixation) and performance metrics for all WM loads in younger and older adults (table 1).

Table 1. Coefficients for correlations between RT and accuracy and alpha power during encoding and retention, relative to fixation, at all WM loads for younger (YA) and older (OA) adults.

		Encoding (YA)		**Encoding (OA)**		**Retention (YA)**		**Retention (OA)**	
		RT	Accuracy	RT	Accuracy	RT	Accuracy	RT	Accuracy
Load-1	*rho*	-0.17	0.16	0.10	-0.20	-0.16	0.01	0.015	-0.22
	p	0.43	0.46	0.62	0.34	0.45	0.95	0.94	0.28
Load-3	*rho*	-0.21	0.26	-0.09	-0.12	-0.20	-0.01	0.009	-0.15
	p	0.33	0.23	0.68	0.56	0.34	0.65	0.97	0.47
Load-5	*rho*	-0.28	0.13	-0.06	0.16	-0.22	-0.23	-0.02	-0.06
	p	0.18	0.54	0.75	0.43	0.31	0.29	0.92	0.77

4 Discussion

In this study, we investigated age-related differences in visual alpha power and frequency during the encoding and retention phases of WM in response to varying loads. Behaviourally, older adults were slower to respond at all WM loads compared to younger adults, but there were no age differences in accuracy. Overall, both alpha frequency and power were lower in older adults than in younger adults in each stage of the task. 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 Alpha power is modulated by load during the encoding and retention period for both younger and older adults

In both younger and older adults, alpha suppression occurred during the encoding period, 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 (i.e. the presentation of a string of letters), alpha power in visual cortex decreases with attention demands (Rajagovindan and Ding, 2010; Sauseng et al., 2005). This is consistent with the interpretation that alpha activity represents inhibition of task-irrelevant stimuli (Jensen and Mazaheri, 2010): if alpha suppression represents a release of inhibition during attention, a decrease in alpha power during encoding likely reflects an increase in cortical excitability to enhance stimulus processing (Heinrichs-Graham and Wilson, 2015; Klimesch, 1997; Murphy et al., 2019; Romei et al., 2010; Thut et al., 2011). Our results suggest that alpha suppression during encoding follows a similar pattern between age groups but differs due to lower alpha power seen in older adults. 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; Jost et al., 2011). However, even though older adults demonstrated poorer performance with increasing WM load, alpha power during the encoding period did not correlate with task performance at any WM load or between age groups. Therefore, age-related WM deficits may not be related to alpha activity during the encoding period.

In both age groups, we found that alpha power decreased under higher WM loads during the retention period. This is inconsistent with the reliably reported increase in visual alpha power during retention in younger adults completing modified Sternberg tasks that is thought to represent sensory gating of task-irrelevant information (Jensen et al., 2002; Proskovec et al., 2019; Tuladhar et al., 2007; Wang et al., 2016). However, studies involving N-back style tasks (Gevins et al., 1997; Pesonen et al., 2007; Stipacek et al., 2003) have found a decrease in alpha power with increases in load. These differences in results are likely due to the nature of the WM tasks. N-back tasks involve an overlapping encoding and retention period where information must be continually updated and maintained, whereas modified Sternberg tasks delineate WM phases such that encoding and retention can be investigated separately. Given that our results align with the findings from N-back style tasks, it is likely that the alpha suppression observed during the retention period of our study is not related to sensory gating or distractor suppression processes. This could be due to the absence of a stimulus during the retention period to act as a distractor or break WM rehearsal, as participants may not have had to engage the neural strategy of increasing visual alpha power to gate irrelevant stimuli. Likewise, the difficulty of our task may not have been conducive to engaging a sensory gating neural strategy, as many participants from both age groups performed near ceiling level for accuracy, and we did not assess the manipulation component of WM (Baddeley, 1992). Therefore, we cannot exclude the possibility that different load-dependent changes in alpha power would have been observed during retention of a more difficult task, or in a task requiring manipulation of items held in WM.

However, alpha activity during the retention period may not solely reflect distractor inhibition. In lateralised 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 (Fukuda et al., 2015). Our results are consistent with these findings, as given that the magnitude of alpha suppression was greatest in load-5 during retention, this pattern of alpha activity may reflect a mechanism for holding multiple items in WM, rather than distractor suppression in this case.

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 to align with the Compensation-Related Utilisation of Neural Circuits Hypothesis (CRUNCH) (Reuter-Lorenz and 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, age-related differences in alpha power at rest may explain this finding, as it may not be physiologically feasible for older adults to modulate visual alpha power in a range that is behaviourally advantageous during WM. Although the task differed, similar findings were described in a study employing a change detection paradigm, where younger adults were found to modulate visual alpha power during WM to suppress distracting information, but older adults did not, even though they performed the task successfully (Vaden et al., 2012). Therefore, increasing visual alpha power as a sensory gating mechanism may not be a valid strategy to facilitate WM performance in older adults. Conversely, 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. As such, clarifying the role of alpha suppression during WM and cognitive ageing 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 8-12Hz) 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 suggest that when alpha power is calculated based upon individual peak alpha frequency, the pattern of alpha activity seen in older adults across WM phases appears similar to that of younger adults, although alpha power was lower in older adults across all loads and phases of the task. However, this age-related reduction in power was not associated with RT or accuracy on the task, suggesting that decreases in alpha power may not contribute to age-related decline in WM performance.

4.2 Age, task and load modulation of alpha frequency

In this study, we demonstrated a decrease in alpha frequency with age. Age has long been known as one of the most important factors influencing the frequency of the alpha rhythm (Dustman et al., 1985; 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. Previous work has demonstrated intra-individual variation in alpha frequency during WM performance, which was interpreted to represent activation of different alpha networks based on task demands (Klimesch, 1997). 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). Likewise, using a modified Sternberg task similar to that of the current study, it was shown that alpha frequency decreased with load during the encoding period, and increased with load during the retention period in younger adults (Babu Henry Samuel et al., 2018). Here, we have shown that alpha frequency is modulated by load and task performance in a similar manner in both younger and older adults during encoding and retention, although these task-related changes in peak frequency did not correlate with WM performance.

During the encoding and retention periods, we observed a load-dependent increase in peak frequency, suggesting that alpha frequency reflects cognitive engagement or is a metric of cognitive load that is common to both younger and older adults.

Considering alpha activity is associated with inhibitory processes, slower alpha frequency would allow for longer windows of suppression (Jensen and Mazaheri, 2010; Sadaghiani and Kleinschmidt, 2016), which may facilitate protection against interference during WM. Our results partially support this idea. According to this interpretation, the increase in alpha frequency seen during encoding may reflect a release of inhibition to facilitate information processing, which is consistent with the decrease in alpha power observed during encoding in this study. However, the fact we also observed load-dependent increases in frequency during retention may invalidate this theory, as higher alpha frequency during retention would be counterproductive to performance. This was shown in a recent study which demonstrated that higher peak frequency during retention led to slower RT (Babu Henry Samuel et al., 2018). Despite seeing this pattern of results, individual alpha frequency at each task time point and load did not correlate with better performance in each age group. As such, determining the task-relevance of alpha peak frequency during WM presents an avenue for future research.

4.3 Conclusion

Although the alpha rhythm slows with age and decreases in power, both alpha power and frequency were modulated in a similar task- and load-dependent manner during WM performance in both younger and older adults. However, these changes in alpha were not associated with task performance. Future research should elaborate the functional significance of alpha power and frequency changes that accompany WM performance in cognitive ageing.

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Declarations of interest

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

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