Resting-State EEG Aperiodic Exponent Moderates the Association Between Age and Memory Performance in Older Adults

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Abstract

Memory functions are susceptible to age-related cognitive decline, making it essential to explore the underlying neurophysiological mechanisms that contribute to memory function during healthy ageing. Resting-state EEG (rsEEG) parameters, particularly the aperiodic exponent, a marker of cortical excitation-inhibition balance, and individual alpha frequency (IAF), a correlate of neural processing efficiency, have demonstrated associations with ageing and cognitive functions. This study investigated associations between these rsEEG markers and performance across multiple memory systems in healthy older adults (n = 99) aged 50-84 years, specifically the moderating and mediating effects on memory and age-memory relationships across episodic, working, and visual short-term memory systems, assessed via computerised tasks. Results revealed significant moderating effects of the aperiodic exponent on age-related performance in episodic (EM) and visual short-term memory (VSTM). Notably, for individuals with a higher exponent, age was not significantly associated with EM or VSTM performance, whereas those with average and lower exponent values showed poorer performance with older age. These findings suggest that average and lower aperiodic exponents may reflect a marker of decrement in age-related memory performance and higher exponents may index an underlying protective mechanism against age-related memory decline. This investigation extends the current understanding of cognitive ageing mechanisms by identifying the aperiodic exponent as a potential biomarker explaining individual differences in cognitive ageing trajectories in older adult populations, particularly in EM and VSTM systems, and establishes a framework for studying neuroprotective mechanisms and developing interventions to preserve cognitive function in older adults.

Keywords

Electroencephalography; Age; Periodic; Alpha; Aperiodic; Cognition; Memory

1.0 Introduction

Cognitive decline represents a well-documented feature of normal ageing (Ferguson et al., 2021; Salthouse, 2009), with memory systems exhibiting particularly pronounced vulnerability to age-related deterioration (Nyberg et al., 2012; Raz & Lindenberger, 2011; Salthouse, 2011). Multiple memory systems demonstrate systematic changes across the ageing process: episodic memory (EM), which encompasses the encoding, maintenance, and retrieval of temporally and spatially contextualised personal experiences (Tulving, 2002); working memory (WM), characterised by the active maintenance and manipulation of task-relevant information in the absence of ongoing sensory input (Baddeley, 2012); and visual short-term memory (VSTM), defined by the capacity-limited temporary storage of visual representations (Logie, 1989; Luck & Vogel, 1997; Phillips, 1974). These memory systems, fundamental to higher-order cognitive functions, demonstrate significant age-associated declines (Brockmole & Logie, 2013; Nyberg et al., 2012; Nyberg & Pudas, 2019; Park et al., 2002; Park & Reuter-Lorenz, 2009; Salthouse, 1991, 2009). Together, these observations underscore the importance of understanding the underlying neurophysiological mechanisms that contribute to memory function throughout the healthy ageing process, particularly among older adults. Such understanding may facilitate identification of factors that promote cognitive resilience or accelerate decline, thereby informing the development of targeted interventions designed to preserve cognitive function in ageing populations.

Electroencephalography (EEG) provides a high-temporal resolution, non-invasive measurement of neural activity that enables detailed investigation of neurophysiological processes. The signals captured through EEG comprise both periodic (oscillatory) and aperiodic (non-oscillatory) components, which together reflect the brain's overall dynamics. Among the oscillatory activities, alpha rhythms (8–12 Hz) have been extensively studied in the context of cognitive function and ageing-related processes (Babiloni et al., 2006; Başar, 2012; Başar & Güntekin, 2012; Klimesch, 1999; Michels et al., 2013; Scally et al., 2018).

Individual alpha peak frequency (IAF), defined as the peak frequency within an individual's alpha

band, represents a key periodic EEG marker demonstrating associations with ageing and cognitive

functions, such as attention (Angelakis et al., 2004; Campbell et al., 2024; Klimesch et al., 2007;

Ramsay et al., 2021), memory (Benedek et al., 2014; Klimesch, 1997; Wianda & Ross, 2019), and

information processing speed (Cesnaite et al., 2023; Klimesch et al., 1996). IAF demonstrates

systematic developmental modulation across the lifespan, characterised by an increase from childhood

to adolescence (Cragg et al., 2011; Klimesch, 1999; Tröndle et al., 2022) and subsequent decline from

adulthood into older age (Campbell et al., 2024; Cesnaite et al., 2023; Finley et al., 2022; Ishii et al.,

2018; Knyazeva et al., 2018; Mizukami & Katada, 2018; Smith et al., 2023). This modulation with

age is thought to reflect underlying neurobiological changes, particularly decreases in white matter

integrity associated with ageing (Valdés-Hernández et al., 2010). Individuals with a higher IAF across

adulthood and older age demonstrate positive associations with multiple domains of cognitive

function, including WM performance (Cesnaite et al., 2023; Klimesch, 1997; Richard Clark et al.,

2004), sustained attention capacity (Campbell et al., 2024) and cognitive preparedness (Angelakis et

al., 2004). Furthermore, a faster IAF has demonstrated correlations with general intelligence (Grandy,

Werkle-Bergner, Chicherio, Lövdén, et al., 2013). While oscillatory activity like IAF provides

important insights into cognitive function, non-oscillatory components of neural activity are also

crucial to consider.

Regarding the non-oscillatory components of neural activity, the aperiodic activity (sometimes

referred to as "background noise") is characterized by a 1/f-like distribution. This distribution reflects

a systematic decrease in power as frequency increases. The exponent of this activity corresponds to

the negative slope of the power spectra when plotted on a log-log scale and is purported to reflect the

excitation/inhibition (E:I) balance (Gao et al., 2017). Recent work has shown systematic age-related

alterations of the exponent, with older adults generally exhibiting a reduced (flatter) exponent when

compared to younger adults (Dave et al., 2018; Merkin et al., 2022; Tran et al., 2020; Tröndle et al.,

2023; Voytek et al., 2015) and across the lifespan (Thuwal et al., 2021). However, studies focusing

specifically on older adult populations have yielded mixed findings regarding age-associated changes

in the exponent. While some studies report a decrease in the exponent within older age ranges (Cesnaite et al., 2023; Finley et al., 2022), others fail to identify significant associations (Campbell et al., 2024; Merkin et al., 2022; Smith et al., 2023). This may be due to sample size, with studies reporting significant age-related effects typically having substantially larger cohorts (Cesnaite et al., 2023; Finley et al., 2022) compared to the studies finding no significant relationships (Campbell et al., 2024; Merkin et al., 2022; Smith et al., 2023), suggesting that age-associated changes in the exponent during later life may represent subtle effects.

Recent research has uncovered connections between the aperiodic exponent and multiple cognitive functions, including lexical prediction (Dave et al., 2018), WM (Ouyang et al., 2020), and interference processing (Kałamała et al., 2024) during task, as well as cognitive speed (Montemurro et al., 2024; Ouyang et al., 2020) and WM (Thuwal et al., 2021) at rest. However, studies examining resting-state aperiodic activity's relationship with cognitive function across adulthood and specifically within older populations remains in early stages, producing mixed findings. While several studies have shown associations between the exponent and cognitive performance metrics in older adults, both-cross sectionally (Smith et al., 2023) and longitudinally across the adult lifespan (Finley et al., 2024), other studies have failed to replicate these relationships (Campbell et al., 2024; Cesnaite et al., 2023; Tröndle et al., 2023).

The inconsistency may stem in part from the potential limitations of traditional neuropsychological assessments. Conventional pen-and-paper and verbal assessments are often static, low-dimensional measures of cognition (Pitkow & Angelaki, 2017), such that they typically assess a limited number of constructs with simple stimuli and basic response formats. Furthermore, examiner-administered assessments may introduce potential sources of variability through scoring inconsistencies and examiner bias. In contrast, computerised cognitive assessments offer several enhanced methodological advantages, particularly for investigating cognitive function in ageing populations. These include increased sensitivity and precision, automated scoring and interpretation, greater standardisation, alternating forms of tasks to minimise practice effects and the ability to measure a

broader range of cognitive processes (Gates & Kochan, 2015; Parsons et al., 2018; Wild et al., 2008; Zygouris & Tsolaki, 2015).

In our previous study, which examined resting-state EEG (rsEEG) correlates of sustained attention in healthy older adults (50–84 years), we identified distinct relationships between neurophysiological parameters and performance on computerised sustained attention tasks (Campbell et al., 2024). IAF emerged as a key neural correlate, exhibiting positive associations with performance on the Sustained Attention to Reaction Task (SART; Robertson et al., 1997) and mediated age-related performance effects. However, our previous investigation did not examine memory function within the studied cohort. The current literature investigating relationships between rsEEG IAF, the exponent and memory performance within healthy older adult cohorts are limited, demonstrate conflicting findings and are primarily based on traditional non-computerised neuropsychological assessments (Cesnaite et al., 2023; Finley et al., 2024; Smith et al., 2023; Tröndle et al., 2023). This represents a significant gap in understanding the relationship between rsEEG markers and memory function in older age.

To address this gap and extend our previous work on rsEEG correlates of sustained attention in a healthy older cohort, the present study conducted an exhaustive investigation on how the aperiodic exponent, IAF and age relate to performance on a battery of computerised memory tasks using the Cambridge Automated Neuropsychological Test Battery (CANTAB; Cambridge Cognition Ltd., 2015), targeting different memory systems in the same sample of older adults. More specifically, the aims of the present study were to: (i) explicate direct associations between the rsEEG measures and performance across multiple computerised memory systems in healthy older adults; (ii) assess potential moderating effects of rsEEG measures on age-memory performance relationships.

We hypothesised positive associations between memory performance across all tasks and both IAF and the $1/f$ exponent. Furthermore, we anticipated significant interaction effects between age and these rsEEG markers in predicting memory performance across all tasks. Specifically, we hypothesised that the relationship between age and performance on each memory task would be more pronounced (e.g., poorer memory performance with advancing age) at lower exponent and IAF

values. By incorporating both oscillatory and aperiodic rsEEG markers in conjunction with sensitive, computerised memory assessments, this study sought to advance the current understanding of the relationships between neural dynamics, age and memory function in healthy older adults.

2.0 Methods

2.1 Participants

The cross-sectional analysis in this study utilised data from 99 healthy individuals aged 50 to 84 years from the Lifestyle Intervention Study for Dementia Risk Reduction (LEISURE). LEISURE, an ongoing study based at the University of the Sunshine Coast's Thompson Institute, has its full protocol published separately (Treacy et al., 2023). In summary, participants were recruited from the community, aged 50-85, fluent in English, and generally in good health. Exclusion criteria included diagnosed psychiatric or major neurological conditions, mild cognitive impairment, significant head trauma history (loss of consciousness>60 min), stroke, epilepsy, or current use of psychotropic drugs. The study's protocol received approval from the University's Human Research Ethics Committee (A191301) and was registered with the Australian New Zealand Clinical Trials Registry (ACTRN12620000054910). All participants provided written informed consent before their involvement in the study.

2.2 Experimental Procedure

As previously published (Campbell et al., 2024), participants first completed the CANTAB battery. The rsEEG assessment was generally conducted the next day or, if not possible, within the same week.

2.3 Cognitive Battery

Participants were individually assessed using the CANTAB (Cambridge Cognition Ltd., 2015) on an iPad touchscreen interface. Three neuropsychological tasks were selected from the battery completed

by the participants to evaluate memory functions: Delayed Matching to Sample (DMS), Paired

Associates Learning (PAL) and Spatial Working Memory (SWM).

The DMS task, lasting approximately 7 minutes, assesses visual simultaneous and short-term

memory. Participants are presented with a complex visual pattern and then asked to select the

matching pattern from four similar options. These options are displayed either simultaneously or after

a delay of 0, 4, or 12 seconds following the disappearance of the original pattern. The primary

outcome measure is Percent Correct All Delays (DMS PCAD), representing the percentage of

assessment trials containing a delay during which the subject chose the correct box on their first box

choice. Higher scores indicate better performance.

The PAL task, lasting approximately 8 minutes, assesses visuospatial EM and learning. Participants

are presented with containers arranged around the edge of the display, which open randomly to reveal

complex visual patterns. Subsequently, the patterns appear one by one in the center of the screen, and

participants must select the original container associated with each pattern. The difficulty level

increases progressively from 2 to 8 containers. Participants must complete each level without errors to

progress; failing four times at any level ends the test. The primary outcome measure is Total Errors

Adjusted (PAL TEA), which is the total number of errors across all assessed trials and stages,

adjusted for incomplete or failed trials (assuming 95% error and 5% correct by chance for remaining

stages). Lower scores indicate better performance.

The SWM task, lasting approximately 4-6 minutes, assesses spatial WM. Participants are presented

with a series of boxes and must tap them to find a hidden token. In each trial, participants must avoid

revisiting boxes where a token has already been found. The number of boxes increases progressively

from four to six and finally to eight. The colour and position of the boxes vary with each trial to

prevent learning effects. The primary outcome measure is Total Between-Search Errors (SWM BE),

which is the number of times the participant returns to a box in which a token has already been found

across all trials. Lower scores indicate better performance.

2.4 Electrophysiological Recordings

rsEEG data were acquired using a 32-channel Active-Two BioSemi system (BioSemi Active-Two, V.O.F., Amsterdam, Netherlands) during four-minutes of eyes-closed resting state. For comprehensive details of the data acquisition protocol, readers are referred to Campbell et al., (2024).

2.5 Electroencephalographic Analysis

2.5.1 Signal Pre-processing

Signal preprocessing followed procedures are detailed in Campbell et al., (2024). Briefly, the data underwent offline referencing to the common average reference, band-pass filtering (1-30 Hz), and artifact rejection using MNE Python (Gramfort et al., 2013) and Autoreject (Jas et al., 2016, 2017) as well as segmentation into 5-second epochs without overlap.

2.5.2 Spectral Analysis

The spectral analysis involved two main steps: calculating the power spectrum density (PSD) of the rsEEG signals and decomposing the PSD into periodic and aperiodic signal components. Initially, the preprocessed rsEEG data were converted to the frequency domain by estimating PSDs using Welch's method (Welch, 1967). This was done for the 1-30 Hz range, employing a 2.5-second Hamming window with 50% overlap and 97.5-second zero-padding. The extended zero-padding allowed for finer interpolation in the frequency domain, enabling a more precise estimation of IAF to 0.1 Hz accuracy while acknowledging this doesn't increase true frequency resolution. Average PSD values ($\mu V2/Hz$) were calculated in bilateral parieto-occipital (P3, Pz, P4, PO3, PO4, O1, Oz, O2) and bilateral fronto-central (F1, Fz, F2) regions of interest (ROI). The parieto-occipital ROI was selected based on prior scientific literature, which highlights prominent age-related patterns in the alpha domain (Babiloni et al., 2006; Grandy, Werkle-Bergner, Chicherio, Schmiedek, et al., 2013; Klimesch, 1999; Knyazeva et al., 2018; Mizukami & Katada, 2018; Rossini et al., 2007; Scally et al., 2018; Sghirripa et al., 2021) and aligning with recent studies employing similar measures (Donoghue

et al., 2020; Montemurro et al., 2024; Tröndle et al., 2022, 2023). The fronto-central ROI selection

was guided by emerging evidence demonstrating its significance in cognitive ageing processes

(Khalilian et al., 2024) and aligns with recent studies employing similar spectral measures (Cesnaite

et al., 2023; Finley et al., 2024; Montemurro et al., 2024). Additionally, a recent study has established

an association between aperiodic activity in frontal regions and declining performance in processing

speed and executive function domains (Pathania et al., 2022).

Subsequently, the 'specparam' toolbox (Donoghue et al., 2020) was used to isolate the aperiodic

component of the spectra from the log-transformed regional PSDs. The 'fixed' aperiodic mode was

selected based on visual inspection of the log-log space output, which showed no distinct 'knee' in the

power spectrum. The algorithm settings were: peak width limits (1-12 Hz), unlimited maximum

number of peaks, minimum peak height (0.05 dB), peak threshold (2 standard deviations), and fixed

aperiodic mode. Parameterisation was performed across the 1-30 Hz frequency range. The final step

involved flattening the spectrum by removing the aperiodic component from the original spectrum.

Within the flattened spectrum, the peak with maximum power was identified in the 7-14 Hz range,

and the IAF was extracted.

Preprocessing and spectral analysis were implemented using a custom-developed EEG data

processing pipeline. The specific code is publicly available in the EEG-notebooks GitHub repository

(https://github.com/aliciajcampbell/EEG-notebooks).

2.5.3 Exclusion Criteria

Prior to statistical analyses, rsEEG data were excluded based on the following criteria:

1. *Insufficient artifact-free data.*

If the signal contained less than 50% artifact-free data after global and/or local artifact rejection, i.e.,

< 24 remaining epochs out of the total 48 (n = 1).

2. *Poor spectral fit.*

If the fit of the parameterised power spectrum to the original PSD was below $R^2 < 0.9$ (n=3 in the fronto-central ROI) or contained significant omissions of signal, as determined by visual inspection (n=4 in the fronto-central ROI and n=3 in the parieto-occipital ROI).

   3. Absence of alpha peak.

If no alpha peak was detected, the IAF measure was excluded from the analyses. However, the aperiodic component was retained (n=3 with no peaks in the fronto-central ROI and n=3 with no peaks in the parieto-occipital ROI).

2.6 Statistical Analyses

Statistical analyses were performed using Python scripts, utilising: Pandas (McKinney, 2010; The pandas development team, 2023), NumPy (Harris et al., 2020), SciPy (Virtanen et al., 2020), Pingouin (Vallat, 2018), Statsmodels (Seabold & Perktold, 2010), HLR (Anijärv et al., 2024), Matplotlib (Caswell et al., 2023; Hunter, 2007), Seaborn (Waskom, 2021) and Statannotations (Charlier et al., 2022).

Outliers were identified using z-scores, such that z-scores >3 or <3 were considered extreme cases. Outlier adjustment was performed as required using the z-score standard deviation transformation method, whereby extreme cases were adjusted to one unit above or below the nearest value existing within acceptable z-score ranges (Tabachnick & Fidell, 2013). One univariate outlier was adjusted in the IAF data in the fronto-central ROI, one univariate outlier was adjusted in the SWM BE data and one univariate outlier was adjusted in the education data. Skewness and kurtosis values for raw and outlier corrected variables are provided in Supplementary Material (Table S1).

Gender and handedness were coded as binary variables, with gender coded as 0 for male and 1 for female, and handedness coded as 0 for non-right-handed and 1 for right-handed. Continuous variables were z-scored for statistical analysis.

Descriptive statistics for continuous variables were reported as mean, standard deviation, and range (minimum-maximum), and categorical variables reported as N. Additionally, to assess the pattern of correlation among variables of interest, bivariate correlations between age memory scores and rsEEG measures were calculated using Spearmans Rho (two-tailed). To account for multiple comparisons, *p*-values were corrected using false discovery rate (FDR) at .05 across all pairwise comparisons (Benjamini & Hochberg, 1995). Statistical significance was determined using an alpha level of .05.

The relationship between rsEEG measures and performance across each memory task was examined using independent hierarchical linear regression (HLR) models. These models first assessed the direct associations between two specific rsEEG measures—namely, the exponent and IAF—on performance in the memory tasks. Next, to assess whether the rsEEG measures of interest moderated age-related differences in performance across memory tasks, interaction effects between age and each rsEEG measure were evaluated. Each regression treated a single rsEEG measure as the primary predictor, with each memory task score as the dependent variable. In constructing the HLR models, demographic variables, including age (at the time of EEG recording), gender, years of education and handedness were controlled for in the first step. The rsEEG measure of interest was added in the second step, and the interaction between age and the rsEEG measure was introduced in the third step. Statistical significance was determined using an alpha level of .05.

To further explore significant interaction terms identified in the HLR models, simple slope analyses were conducted. These analyses examined the relationship between age and task performance at three levels of the individual rsEEG measure: low (≤-1 SD below the mean), mean (±1 SD) and high ($\geq+1$ SD above the mean). The simple slopes were calculated using the regression coefficients for the z-scored variables and the significant interaction term, with standard errors derived from the covariance matrix.

3.0 Results

3.1 Descriptive Analyses

1 We have analysed data of 99 participants (M_{age} = 65.47, SD = 8.3; 80 females). Demographic and

2 sample information can be seen in Table 1.

3 **Table 1.** Sample descriptives.

Variable	N	M (SD)	Min, Max
Age (years)	99	65.47 (8.30)	50.16, 84.04
Gender			
Female	80		
Male	19		
Education (years)	99	14.78 (2.84)	9.00, 19.00
Handedness			
Right	86		
Left/ambidextrous	13		
DMS PCAD	99	83.44 (12.02)	47.00, 100.00
PAL TEA	99	19.60 (14.63)	0.00, 57.00
SWM BE	99	17.40 (7.47)	0.00, 30.00
Fronto-central ROI			
IAF	88	9.64 (1.15)	7.00, 12.32
Exponent	91	0.94 (0.21)	0.42, 1.56
Parieto-occipital ROI			
IAF	92	9.74 (1.09)	7.03, 11.9
Exponent	95	0.93 (0.19)	0.50, 1.36

4 M, mean; SD, standard deviation; DMS PCAD, Delayed Match to Sample percent correct (all delays);

5 PAL TEA, Paired Associates Learning total errors (adjusted); SWM BE, Spatial Working Memory

6 between errors; ROI, region of interest.

Bivariate correlations, shown in Figure 1, revealed significant associations between age and performance measures across the memory tasks. Specifically, age exhibited significant positive associations with PAL total errors (adjusted) and SWM between errors, suggesting poorer performance across these tasks with increasing age. Age exhibited a negative association with DMS percent correct (all delays), however, this association did not survive correction for multiple comparisons. Among the scores across memory tasks, SWM between errors showed a positive association with PAL total errors (adjusted). No other significant associations were observed between the memory task scores.

Regarding the rsEEG measures, IAF in the fronto-central ROI showed a significant negative association with age. Similarly, IAF in the parieto-occipital showed a negative association with age, however, this association did not survive correction for multiple comparisons. The exponent in both ROIs did not exhibit significant age-related associations. Within the rsEEG measures, IAF in the fronto-central ROI exhibited a negative association with the exponent in the parieto-occipital ROI. Additionally, IAF values demonstrated significant positive correlations between fronto-central and parieto-occipital ROIs. Similarly, the exponent showed significant positive correlations between fronto-central and parieto-occipital ROIs.

Regarding rsEEG and memory performance relationships across tasks, initially, IAF in the parieto-occipital ROI showed an association with SWM between error scores, however, this association also did not survive correction for multiple comparisons. Thus, no significant associations were observed between rsEEG measures and memory performance across tasks.

Figure 1. Spearman Rank correlation coefficients (ρ) (coloured by magnitude) between performance

across memory tasks, age and resting-state rsEEG measures, with p-values provided in parentheses; p-

values were corrected using false discovery rate (FDR) at .05 across all pairwise comparisons.

Statistical significance was determined using an alpha level of .05; DMS PCAD, Delayed Match to

Sample percent correct (all delays); PAL TEA, Paired Associates Learning total errors (adjusted);

SWM BE, Spatial Working Memory between errors; FC, fronto-central; PO, parieto-occipital; IAF,

Individual alpha peak frequency.

3.2 Hierarchical Linear Regressions

3.2.1 Direct Associations

To examine if the rsEEG measures of interest were directly associated with performance across memory tasks after controlling for demographic variables entered in step 1, we analysed the rsEEG measure added in step 2 of the HLR models.

For fronto-central rsEEG measures, the addition of IAF in step 2 did not significantly improve the overall model fit for DMS percent correct (all delays) scores ($\Delta F = .097$, $p = .756$), PAL total errors (adjusted) scores ($\Delta F = .026$, $p = .872$) or SWM between error scores ($\Delta F = .306$, $p = .581$). Similarly, the addition of the exponent in step 2 did not significantly improve the overall model fit for DMS percent correct (all delays) scores ($\Delta F = .881$, $p = .350$), PAL total errors (adjusted) scores ($\Delta F = .107$, $p = .745$) or SWM between error scores ($\Delta F = .063$, $p = .802$).

For parieto-occipital rsEEG measures, the addition of IAF at step 2 showed no significant predicted improvement for DMS percent correct (all delays) scores ($\Delta F = .096$, $p = .758$), PAL total errors (adjusted) scores ($\Delta F = 1.032$, $p = .313$) or SWM between error scores ($\Delta F = 1.825$, $p = .180$). Similarly, the exponent did not significantly enhance model prediction for DMS percent correct (all delays) scores ($\Delta F = .301$, $p = .584$), PAL total errors (adjusted) scores ($\Delta F = <0.001$, $p = .997$) or SWM between error scores ($\Delta F = .009$, $p = .924$).

Collectively, neither rsEEG measure in each ROI contributed significantly to explaining memory performance in each task after adjusting for demographic variables in the models.

3.2.2. Interaction Effects (Moderation)

To examine if the rsEEG measures of interest moderated age-related differences in performance across memory tasks, HLR models assessed moderation effects by testing age $\times$ rsEEG interactions added in step 3.

For fronto-central measures, the age $\times$ exponent interaction term showed a significant positive association with DMS percent correct (all delays) (standardised $\beta = .221$; $p = .034$) scores, accounting for a 4.7% increase in explained variance and significantly improved the overall model fit ($\Delta F =$

4.626; $p = .034$). This suggests that the fronto-central exponent moderates age effects on DMS

accuracy. Notably, no significant moderation emerged for fronto-central exponent effects on PAL (ΔF

$= .723$; $p = .398$) or SWM (ΔF $= .259$; $p = .612$) scores, nor for fronto-central IAF interactions across

DMS (ΔF $= .591$; $p = .444$), PAL (ΔF $= .665$; $p = .417$) or SWM (ΔF $= .222$; $p = .639$) scores.

For parieto-occipital measures, the age $\times$ exponent interaction showed a significant negative

association with PAL total errors (adjusted) scores (standardised $\beta = -.220$; $p = .028$), accounting for

a 4.6% increase in explained variance and significantly improved the overall model fit (ΔF $= 4.997$, p

$= .028$). This suggests that the parieto-occipital exponent moderates age effects on PAL errors.

Notably, no significant moderation occurred for parieto-occipital exponent effects on DMS (ΔF $=$

3.261; $p = .074$) and SWM (ΔF $= .054$; $p = .818$) scores and parieto-occipital IAF interactions failed

to reach significance for DMS (ΔF $= .251$; $p = .617$), PAL (ΔF $= 1.237$; $p = .269$) or SWM (ΔF $=$

2.671; $p = .106$) scores.

Significant models can be seen in Table 2, while statistics for all models are provided in the

Supplementary Material (Table S2 and Table S3) for further reference.

Table 2. Hierarchical linear regression models predicting memory task performance from main

effects of fronto-central IAF and aperiodic exponent values and interactions with age, including

demographic covariates as step 1 regressors (significant models only).

Dependent Variable	Predictors	Step	β	R^2	F
DMS PCAD	Age	1	-.220*	.084	1.981
	Gender		-.029		
	Education		.057		
	Handedness		-.138		
	Fronto-central exponent	2	-.099	.094	1.759
	Age × fronto-central exponent	3	.221*	.141	2.294*
PAL TEA	Age	1	.314**	.141	3.692**

	Step	β		
Gender		-.072		
Education		-.106		
Handedness		.103		
Parieto-occipital exponent	2	<.001	.141	2.921*
Age × parieto-occipital exponent	3	-.220*	.187	3.377*

β, standardised beta; "Step" outlines which level of the HLR analyses the variables were entered; DMS PCAD, Delayed Match to Sample percent correct (all delays); PAL TEA, Paired Associates Learning total errors (adjusted); *$p < .05$, **$p < .01$, ***$p < .001$.

3.3 Simple Slope Analyses

Simple slope analyses probed the conditional effects of age on memory tasks performance at distinct levels (low, ≤ -1 SD below the mean; mean, ± 1 SD; high, $\geq +1$ SD above the mean) of the moderating rsEEG measures identified in step 3 of the significant HLR models.

For the fronto-central exponent's moderation of DMS percent correct (all delays) scores, age showed significant negative associations at low ($p = .003$) and mean ($p = .019$) exponent levels, but not at high levels ($p = .877$), suggesting that the negative effect of age on DMS accuracy attenuates as the fronto-central exponent increases (Table 3; Figure 2A). Similarly, for the parieto-occipital exponent's moderation of PAL total errors (adjusted) scores, age showed significant positive associations at low ($p = <.001$) and mean ($p = .002$) exponent levels, with no significant age effects observed at high levels ($p = .535$), suggesting that the positive effect of age on PAL errors attenuates as the parieto-occipital exponent increases (Table 3; Figure 2B).

Together, these patterns highlight the moderating role of the fronto-central exponent in the relationship between age and DMS performance, as well as the moderating role of the parieto-occipital exponent in the relationship between age and PAL performance.

Table 3. Simple slopes analysis results for age-related associations in memory task performance moderated by low (≤ -1SD), mean (± 1 SD), and high (≥ 1 SD) levels of the exponent.

DMS percent correct (all delay)

Region	Exponent level	n	Slope	SE	T	CI
	Low (≤−1 SD)	12	−0.492	0.159	−3.088**	−0.809, −0.175
Fronto-central	Mean (±1 SD)	65	−0.257	0.107	−2.393*	−0.470, −0.043
	High (≥1 SD)	14	−0.021	0.148	−0.143	−0.314, 0.272

PAL total errors (adjusted)

Region	Exponent level	n	Slope	SE	T	CI
	Low (≤−1 SD)	16	0.553	0.147	3.774***	0.262, 0.845
Parieto-occipital	Mean (±1 SD)	63	0.321	0.100	3.203**	0.122, 0.520
	High (≥1 SD)	16	0.089	0.142	0.624	−0.194, 0.371

Slopes derived from hierarchical linear regression (step 3 models). SE, standard error; CI depicts 95%

confidence intervals; DMS, Delayed Match to Sample; PAL TEA, Paired Associates Learning; *$p <$

.05, **$p < .01$, ***$p < .001$.

Figure 2. Age associations with memory task performance moderated by resting-state aperiodic

exponents. (A-B) Scatter plots with regression lines show relationships between age (z-scored, x-axis)

and model-predicted task performance (y-axis; hierarchical linear regression, step 3). (A) DMS PCAD

predicted scores. (B) PAL TEA. Coloured lines indicate simple slopes for aperiodic exponent groups: Low ($\leq$−1SD, blue), Mean ($\pm$1 SD, grey), and High ($\geq$1SD, red) in fronto-central (A) and parieto-occipital (B) regions. Shaded bands = 95% confidence intervals. DMS PCAD, Delayed Match to Sample percent correct (all delays); PAL TEA, Paired Associates Learning total errors (adjusted).

4.0 Discussion

The present study aimed to investigate how the aperiodic exponent and IAF, relate to memory performance in healthy older adults. Specifically, we examined whether these neural measures were associated with performance on computerised tasks from the CANTAB battery that target various memory systems, including visual short-term memory (DMS), episodic memory (PAL) and spatial working memory (SWM), and whether they moderated or mediated the relationship between age and memory performance. While we found no evidence for direct associations within the HLR models, moderation analysis via interaction terms in the HLR's and simple slope analyses revealed that the aperiodic exponent moderated the association between age and performance on the VSTM (DMS) and EM (PAL) tasks. Specifically, within this cross-sectional sample, older adults with a lower exponent showed a stronger negative association between age and memory performance, whereas those with a higher exponent showed a less pronounced age-related association.

Recent research has indicated that neural network dynamics, specifically the balance between excitation-to-inhibition (E:I) balance, primarily influenced by the interplay of glutamate-mediated excitation and GABA-mediated inhibition synaptic connections, can be quantified by the aperiodic exponent of the power spectral density (PSD) (Gao et al., 2017; Hong & Rebec, 2012; Waschke et al., 2017). The power distribution in local field potentials (LFPs) reflects this dynamic, such that a steeper or increased exponent represents inhibitory activity dominating over excitatory, and a flatter or decreased exponent represents a shift toward excitation over inhibition (Donoghue et al., 2020; Gao et al., 2017; Wang, 2020). Our findings position the rsEEG aperiodic exponent as a potential biomarker for individual differences in age-associated memory trajectories, such that lower exponents, potentially reflecting excitation-dominant E:I balance, may reflect a marker of decrement in age-

related memory performance, particularly within systems like EM and VSTM where declines are well-documented (Adamowicz, 1976; Brockmole & Logie, 2013; Menegaux et al., 2020; Mitchell & Cusack, 2018; Tromp et al., 2015). Conversely, a higher exponent, reflecting optimal E:I balance through robust inhibitory regulation, may index an underlying protective mechanism against these specific age-associated declines.

It is thought that neural homeostasis in cortical networks requires precise regulation of E:I synaptic transmission (Roudi & Latham, 2007; Shew et al., 2011), serving as a crucial mechanism governing the information processing and behavioural output within the central nervous system (Vogels et al., 2011). Disruptions to this balance, characterised by an increase in glutamatergic transmission or diminished GABAergic inhibition, may precipitate brain circuit and large-scale network dysfunction such as heightened neuronal network excitability potentially compromising social functioning and cognitive performance across multiple domains (López-Sanz et al., 2017; Mendez et al., 2018; Stam et al., 2009). A growing body of research suggests that maintenance of optimal E:I dynamics promotes efficient information encoding (Denève & Machens, 2016), transmission (Shew et al., 2011) and information processing (Kinouchi & Copelli, 2006; Markram et al., 2004; Yizhar et al., 2011), processes fundamental to both EM and VSTM. The present study's finding that the aperiodic exponent moderates the association between age and memory performance in older adults, highlights its potential role as a neurophysiological marker explaining individual differences in cognitive ageing trajectories, particularly in EM and VSTM systems, and offers a potential target for interventions aimed at maintaining memory function in later life. Given the cross-sectional design of the current study, future longitudinal research is warranted to track exponent trajectories in relation to age-related memory decline and investigate causality.

Interestingly, recent studies have reported conflicting findings that differ from ours regarding the interplay between the aperiodic exponent, age, and memory. A large-scale investigation (n = 1073) by Cesnaite et al., (2023) examining older adults (60-80 years) in a similar age range to the present study (50-84 years) failed to demonstrate significant modulatory effects of the exponent on EM

performance, both directly and through interaction with age. The EM measure in this study was derived from an exploratory factor analysis of various cognitive scales. Similarly, Finley et al., (2024) explored the aperiodic exponent and a factor representing EM at baseline or over a ten-year period in participants aged 36–83 (n = 235) and while the interaction between age and exponent on cognitive performance was not tested, reported no association between the aperiodic exponent and EM, though they did find a relationship with executive functioning. A notable methodological difference emerges in the assessment approaches, such that these prior studies employed traditional neuropsychological assessments, such as pen-and-paper and verbal tests, and performance in specific domains quantified through factorial analytical approaches, contrasting with our use of computerised tests.

The implementation of computerised cognitive batteries, specifically the CANTAB, offers enhanced measurement precision and consistency, reducing examiner-related variability and potentially increasing the sensitivity to detect subtle cognitive changes. The CANTAB-PAL has demonstrated effectiveness in EM assessment, having established robust psychometric properties across diagnostic, cultural and linguistic populations (Barnett et al., 2016). The test exhibits strong temporal reliability (Barnett et al., 2016) and has demonstrated strong correlations with both conventional neuropsychological tests (Matos Gonçalves et al., 2018) and functional assessment metrics (Barnett et al., 2016). Additionally, the CANTAB-DMS paradigm has been validated in clinical populations, including individuals with mild cognitive impairment, dementias and Parkinson's disease (Cabral Soares et al., 2014; Campos-Magdaleno et al., 2021; Fowler et al., 1995; Sahakian et al., 1988), supporting its use in cognitive assessment. The enhanced psychometric properties inherent in these computerised assessments may account for the detection of significant interaction effects between the aperiodic exponent and age on EM and VSTM in our investigation, contrasting with the findings reported in studies utilising traditional verbal and pen-and-paper assessment methods.

Interestingly, the interaction effect between age and the aperiodic exponent was not a significant predictor in the SWM task. Research has shown that performance on the PAL and DMS demonstrate selective sensitivity to medial temporal lobe (MTL) functionality (Owen et al., 1995; Torgersen et al.,

2010), particularly hippocampal integrity, which supports both EM processes (Dickerson &

Eichenbaum, 2010; Nyberg et al., 2000) and short-term retention of visual information (Barense et al.,

2007; Lee et al., 2012; Olson et al., 2006; Warren et al., 2012). In contrast, the SWM task

predominantly relies on distributed frontoparietal networks (Courtney et al., 1998; Curtis, 2006;

D'Esposito et al., 1998; Schweinsburg et al., 2005; van Asselen et al., 2006). This raises the

possibility that the exponent may specifically index the vulnerability or resilience of MTL-dependent

cognitive processes to age-related decline, rather than serving as a general marker of cognitive ageing

across all domains, though further investigation utilising multimodal neuroimaging approaches is

warranted to understand the precise neurophysiological mechanisms underlying these domain-specific

effects.

Additionally, the observed interaction effects between the exponent and age demonstrated

topographically distinct patterns across brain regions, implicating the fronto-central ROI for DMS

performance and the parieto-occipital ROI for PAL. A prior study by Pathania et al., (2022) found that

the exponent within frontal regions served as a significant mediating factor in age-related attentional

performance differences between younger and older adults, although statistical comparisons across

brain regions were not conducted. Similarly, while the present study may suggest that distinct neural

networks contribute to the moderating role of the aperiodic exponent in age-related changes in

memory processes, our study design and analyses did not directly compare brain regions. Future

investigations employing statistical comparisons across scalp regions are warranted to investigate the

spatial distribution of age-exponent interactions and their differential impact on distinct memory

processes.

Furthermore, HLR analyses revealed no significant direct associations between the aperiodic

exponent and memory performance. This finding contrasts with recent evidence supporting the

predictive value of the exponent in cognitive performance, particularly in older adult populations

(Smith et al., 2023) and across the lifespan (Finley et al., 2024). However, other investigations have

similarly failed to demonstrate such associations, suggesting complex underlying relationships

(Cesnaite et al., 2023; Tröndle et al., 2023). The current findings indicate that the exponent's influence on cognitive performance may be contextually dependent, manifesting primarily through interactions with age-related factors rather than through direct effects, though further research is required to clarify these findings.

The present study also revealed no significant direct associations between IAF and memory performance across tasks or a significant moderation effect of IAF and age on memory performance. This finding contrasts with recent evidence demonstrating IAF's predictive value for cognitive performance, such as sustained attention in older adults, as per our previous study (Campbell et al., 2024), and longitudinal cognitive decline across middle to late adulthood (Finley et al., 2024). Additionally, prior research has established positive associations between IAF and interference resolution in WM performance within older adults (Cesnaite et al., 2023), making the absence of significant relationships in our study particularly noteworthy. Again, this may be due to methodological differences. The substantially larger sample size employed in the aforementioned study may have provided enhanced statistical power for detecting subtle associations with IAF within this age demographic. Furthermore, methodological differences in WM paradigms warrant consideration, as Cesnaite et al., (2023) investigated interference resolution in WM, whereas the current study examined errors in spatial WM among other memory systems. The spatial distribution of observed effects also differed, with the prior study identifying primarily temporal lobe associations, while the present study focused exclusively on fronto-central and parieto-occipital ROIs. Future investigations should address these discrepancies by incorporating multiple memory paradigms, expanded spatial sampling, and larger cohort sizes.

4.1 Limitations

There are several limitations inherent with our study that require discussion. Firstly, the cross-sectional nature of our study design precluded the determination of causal relationships as well as any longitudinal relationships between neurophysiological parameters and cognitive performance. The sample demographics demonstrate a substantial gender bias with female predominance, restricting

generalisability across gender groups. Our cohort's homogeneity, comprising highly functional and well-educated older adults, may also not adequately represent the broader ageing population, particularly individuals experiencing cognitive decline. Additional methodological limitations include the restricted spatial sampling, with the present study focusing exclusively on fronto-central and parieto-occipital regions. Future research would benefit from comprehensive coverage of other cortical areas or statistical comparisons between regions, as well as additional frequency bands. Additionally, the absence of task-based EEG restricts analysis of state-dependent variations in neural dynamics. Finally, the single-modality neuroimaging approach constrains integration with other age-related neurobiological alterations documented in the literature.

5.0 Conclusion

The present study uncovered key relationships among rsEEG aperiodic exponents, age, and memory function in older adults aged 50-84 years. The findings demonstrate a significant moderating effect of the exponent on age-related performance in both episodic and visual short-term memory systems. Notably, for individuals with higher exponent values, age was not significantly associated with episodic or visual short-term memory performance, whereas those with average and lower exponent values showed poorer episodic and visual short-term memory performance with advancing age. This pattern suggests that average and lower aperiodic exponents may reflect a marker of decrement in age-related memory performance and steeper exponents, potentially reflecting an optimised excitation-inhibition balance within neural circuits, may index a protective mechanism against age-related memory decline. The present findings provide new insights into the neurophysiological mechanisms underlying cognitive ageing and identify the aperiodic exponent as a potential biomarker of individual differences in age-related memory performance trajectories. Finally, our study establishes a theoretical framework for investigating neural mechanisms that may offer protection against age-related cognitive decline, potentially informing the development of interventional approaches targeting preserved cognitive function in older populations and advances the understanding of the complex interplay between neurophysiological parameters and cognitive aging.

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CRediT Authorship Contribution Statement

Alicia J. Campbell: Conceptualisation, Methodology, Software, Formal Analysis, Investigation, Data Curation, Writing-Original Draft, Visualisation; **Toomas Erik Anijärv:** Software, Data Curation, Writing – Review & Editing; **Mikael Johansson:** Conceptualisation, Methodology, Writing – Review & Editing; **Thomas Pace:** Writing – Review & Editing**; Jim Lagopoulos:** Writing – Review & Editing; **Daniel F. Hermens:** Writing – Review & Editing, Supervision; **Jacob M. Levenstein:** Writing – Review & Editing, Supervision; **Sophie C. Andrews:** Conceptualisation, Methodology, Formal Analysis, Writing – Review & Editing, Supervision.

Declaration of competing interest

None.

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