Age Differences in Resting State EEG and their Relation to Eye Movements and Cognitive Performance

Jemaine E. Stacey[1,3], Mark Crook-Rumsey[1], Alexander Sumich[1], Christina J. Howard[1], Trevor Crawford[2], Kinneret Livne[1], Sabrina Lenzoni[1,4], & Stephen Badham[1*]

*Corresponding author: stephen.badham@ntu.ac.uk , +44 (0)115 848 4271

[1]*Department of Psychology, Nottingham Trent University, NG1 4BU, UK*

[2]*Department of Psychology, Lancaster University, LA1 4YF, UK*

[3]*Nottingham Biomedical research Centre, University of Nottingham NG1 5DU, UK*

[4]*Department of Psychology, Pontifical Catholic University of Rio de Janeiro, 22451-900, Brazil*

Supplementary Materials

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Abstract

Prior research has focused on EEG differences across age or EEG differences across cognitive tasks/ eye tracking. There are few studies linking age differences in EEG to age differences in behavioural performance which is necessary to establish how neuroactivity corresponds to successful and impaired ageing. Eighty-six healthy participants completed a battery of cognitive tests and eye-tracking measures. Resting state EEG (n=75, 31 young, 44 older adults) was measured for delta, theta, alpha and beta power as well as for alpha peak frequency. Age deficits in cognition were aligned with the literature, showing working memory and inhibitory deficits along with an older adult advantage in vocabulary. Older adults showed poorer eye movement accuracy and response times, but we did not replicate literature showing a greater age deficit for antisaccades than for prosaccades. We replicated EEG literature showing lower alpha peak frequency in older adults but not literature showing lower alpha power. Older adults also showed higher beta power and less parietal alpha power asymmetry than young adults. Interaction effects showed that better prosaccade performance was related to lower beta power in young adults but not in older adults. Performance at the trail making test part B (measuring task switching and inhibition) was improved for older adults with higher resting state delta power but did not depend on delta power for young adults. It is argued that individuals with higher slow-wave resting EEG may be more resilient to age deficits in tasks that utilise cross-cortical processing.

Keywords: *EEG, eye tracking, working memory, inhibition, ageing*

1. Introduction

Given the rapid rise in the aged population and anticipated increase in socioeconomic burden within the next few decades (United Nations DESA, 2017), understanding age-related change in brain function and cognition is imperative. Some cognitive processes resist age-related decline more than others (Park & Festini, 2017). For example, relative to young adults, older adults experience memory deficits (Craik, & Byrd, 1982) and express difficulty in suppressing and inhibiting information (Hasher & Zacks, 1988), whilst crystallised abilities, such as vocabulary, show little decline with age (Tucker-Drob, Brandmaier, & Lindenberger, 2019; Verhaeghen, 2003). Cognitive ageing, therefore, can be seen at least partly as an adaptive process, with individuals using different strengths and contending with different cognitive deficits throughout their lifespan (Park, & Reuter-Lorenz, 2009; Dennis & Cabeza, 2008). Psychophysiological methods used to understand age differences cognitive function include electroencephalography (EEG) and eye-movement assessment, with mixed findings (Scally et al. 2018; Dustman, Shearer, & Emmerson, 1993). However, it is poorly understood whether age changes in EEG activity represent successful or impaired cognitive ageing (Schmiedt-Fehr et al. 2016). The current study investigated age differences in EEG, cognition and eye-movements, and the relationship between these measures.

The assessment of oculomotor performance in relation to saccades has shown numerous theoretical and clinical insights over the last few decades (e.g., see Smyrnis, 2008, for a review). Key tasks used in this field and the current study are the antisaccade task where a participant must direct their gaze *away* from a target that appears on screen; and the prosaccade task where a participant must direct their gaze *towards* a target that appears on screen. Contrasting antisaccade performance with prosaccade performance allows the comparison of controlled, inhibitory responses to automatic prepotent responses, respectively. Antisaccade dysfunction has been linked to a variety of neurological disorders including Alzheimer's disease (Crawford et al. 2005), schizophrenia (Levy et al., 2010) and schizotypy (Thomas et al., 2021), chronic fatigue syndrome (Badham & Hutchinson, 2013) and attention deficit/hyperactivity disorder (Munoz et al. 2003). With regard to eye-movements in healthy older adults, deficits are typically more evident for tasks involving the suppression of motor activity, such as the antisaccade task in contrast to the prosaccade task, which shows minimal age related decline (Abel & Douglas, 2007; Peltsch et al., 2011). This links closely to key cognitive ageing theory hypothesising an age-related decline in inhibitory processing (Hasher & Zachs, 1988) and attentional control (Kray, Eppinger, & Mecklinger, 2005).

Saccadic performance has been associated with intra- and inter-individual variance in alpha activity (Hamm, Sabatinelli, & Clementz, 2012) and alpha activity has been associated to the coordination and

integration of sensory information with saccadic responses (Sanfim et al. 2012). It is therefore possible that age differences in saccadic performance will correspond to age differences in alpha activity (see below). The connection between ageing, eye movements and neurophysiology is evidenced in an ageing study by Mirsky et al. (2011) who found that antisaccades were related to behavioural measures of executive control and to grey matter volume in two frontal areas (the right supplementary eye field, and left inferior frontal junction). These findings are consistent with (i) an age related deficit in inhibitory control (Hasher & Zachs, 1988) which is a process necessary to supress a tendency to look towards the appearing target, (ii) a prefrontal deficit account of ageing where prefrontal decline is linked to a reduction in executive control (West, 1996), and (iii) research showing frontal lesions impede saccade suppression more than automatic eye movements (Guitton, Buchtel, & Douglas, 1985; Pierrot-Deseilligny et al. 1991).

In Go/No-Go eye movement paradigms, saccades are made towards "go" stimuli and inhibited in response to No-Go stimuli (often determined by location of stimuli). The Go /No-Go task was introduced to enable us to determine whether any age-related change in inhibitory control impairment might be contingent on an additional cognitive load of volitional control. Although the key feature of the NO-GO and the GO/NO-GO paradigms is that they require the inhibition of a prepotent saccade in the 'NO-GO' phase, in contrast to the anti-saccade paradigm for example, which requires a voluntary saccade away from the target, the GO/NO-GO tasks only require a saccade directed towards to the target in the 'GO' phase. Therefore, if the requirement to initiate a volitional saccade is the source of any change in inhibitory control then inhibitory performance should improve in the GO/NO-GO paradigm since the volitional component is reduced, relative to the anti-saccade paradigm. However, if there is no selective effect of inhibitory control then the change in the volitional component should have little effect on inhibition control. EEG studies of the go/nogo task (non-eye-tracked versions of the task) have shown delta and theta activity are linked to inhibitory performance (Harper, Malone, & Bernat, 2014) and modulate age-related differences in performance (De Blasio & Barry, 2018). To our knowledge, the current study is the first to combine ageing, EEG and eye movement analysis in one investigation and this will allow new insights in to behavioural and neurophysiological ageing, including a potential to influence applied clinical research.

1.1 EEG frequency bands in relation to ageing and cognition

1.1.1 Beta Power

Findings regarding beta power are contradictory with some studies reporting decreases in beta activity with age whilst other studies report increases (see Barry & De Blasio, 2017; Caplan, Bottomley, Kang & Dixon, 2015, for further discussion); the latter has been localised to M1 motor cortex. In a review, Dustman et al. (1993) found that beta activity peaks at approximately 60 years of age before

declining. Others have reported an inverted “U” shaped curve of the relationship between amyloid burden and higher frequency activity, including higher band beta activity (Gaubert et al., 2019).

Resting beta activity has been proposed to be associated with the default mode of processing and ongoing cognitive activity outside of task specific processing (Laufs et al., 2003; Mantini et al., 2007). However, Engel and Fries (2010) propose that rather than reflecting “idling” in the resting state, beta activity may be a signature of an active process that promotes the existing motor set whilst compromising neuronal processing of new movements. Thus, spontaneous enhancements of beta band activity have been associated with impaired movement performance, such that voluntary movements triggered during periods of enhanced beta are slowed (Gilbertson et al. 2005). In pathophysiology, excessive beta band activity in the basal ganglia underpins bradykinesia (for review see Engle and Fries, 2010). Whilst this has been interpreted in terms of dopamine function, increased beta power also results from upregulation of GABAergic systems (Rossiter et al., 2014). Beta suppression, on the other hand, has been associated with increased attentional engagement to visual tasks (Bauer et al., 2006; Hoogenboom et al., 2006; Siegel et al., 2008; Scheeringa et al., 2011).

Other authors have argued that beta activity reflects arousal of the visual system and increased attention (Wróbel, 2000). When EEG is measured during tasks requiring attention to visual stimuli, in that increased beta activity relates to increased alertness and shorter reaction times (RTs) to stimuli (Kamiński et al., 2012). Consistent with this, task-related occipital beta activity has been linked to alertness and vigilance in older adults (Gola at al., 2012; 2013) with greater beta activity associated with better performance. Thus, the functional significance of resting state beta activity in relation to typical and atypical aging remains unclear, since lower beta activity could be the cause of poorer performance, but it could also be the result of greater compensatory attentional engagement and effortful processing of stimuli (Dustman et al., 1993).

1.1.2 Alpha Activity

Reductions in alpha power in typical aging have been reported, which may be particularly prominent in the upper alpha band (10-12Hz) and tied to the individual alpha peak frequency (Scally et al., 2018). Thus, such findings may be secondary to a slowing of the alpha peak (Dustman et al., 1993; Scally et al., 2018). Barry and De Blasio (2017) suggest a specific reduction in resting state alpha power at right parietal sites in older relative to younger adults. Parietal alpha during a Posner task, has also recently been shown to mediate the relationship between age and reaction time (Arif et al., 2020).

Alpha power has been proposed as an inverse indicator of arousal during the waking state, as alpha suppression occurs in response to closing the eyes and caffeine ingestion in an additive manner (Barry

and De Blasio, 2017; Klimesch, 2012; Pfurtscheller, Stancák & Neuper, 1996). However, alpha has also been proposed to reflect active inhibition of cortical regions not currently required for any given task. Lower power in the lower frequency occipital alpha band is associated with dysregulation of the visual cortex and the propensity to experience pseudohallucinations under Ganzfeld conditions (Sumich et al., 2018).

Ageing studies that compare resting state EEG with eyes open and eyes closed are sparse. Barry and De Blasio (2017) found that alpha changes between eyes closed and eyes open EEG were smaller for older adults than for young adults, with similar effects seen for other bands (theta, delta, beta). This suggests a reduction in inhibitory control of neurophysiological mechanisms with healthy ageing, which is consistent with behavioural evidence showing inhibitory deficits in healthy older adults (Hasher & Zacks, 1988). Age-related inhibitory deficits might explain decline in working memory which has also been associated with alpha activity. For example, in young adults, alpha power is positively associated with working memory performance (Jensen, Gelfand, Kounios and Lisman., 2002). Additionally, Clark et al. (2004) show that as peak alpha frequency in the frontal regions changes with age (11–70yrs), so too does performance on a working memory task (digit span). Overall, alpha power and peak alpha frequency tend to be positively related to cognitive performance and negatively related to age (Klimesch, 1999; Choi et al., 2019), with more precise associations observed between specific alpha bands and cognitive functions. Memory performance and semantic processing has been associated with larger upper alpha (but less theta and lower alpha power), whereas lower alpha bands are associated with attentional demands that dominate during the encoding of new information (for review see Choi et al., 2019).

1.1.3 Delta and Theta power

Increases (Klimesch, 1999) and reductions (Barry and De Blasio, 2017; Vlahou, Thurm, Kolassa & Schlee, 2014) in slow-frequency activity (ranges below 7 Hz), including delta and theta activity have also been reported as a function of age. In contrast to faster frequencies, slower frequencies show a "U" shaped curve in relation to amyloid load (Gaubert et al., 2019).

Theta activity has previously been proposed to reflect mechanisms underpinning memory, motor, and spatial tasks. There are mixed findings on slow-wave EEG signals in relation to cognition in the context of ageing. Finnigan and Robertson (2011) found increased theta power was associated with higher scores on cognitive tests (verbal recall, attention and executive function) in older adults (as did Kavcic et al., 2016). Whilst Finnigan and Robertson found no relationship between alpha or delta and any of the cognitive tests, electrode array was limited (4 sites) and others have reported inverse associations between delta activity and memory performance in older participants reporting cognitive

problems clinically (Kavcic et al., 2016). In comparison, Vlahou, Thurm, Kolassa & Schlee (2014) use MEG to show increases in delta and theta power were associated with better performance on the Trail making-B task in older adults (>54 years), but not younger adults. In that study, delta and theta activity were also inversely associated with age. In contrast, Roca-Stappung et al. (2012) found that lower values of delta and theta power were related to better cognitive performance in older adults. Similarly, others also report power increases for slower frequency bands in relation to cognitive decline (see Caplan et al., 2015, Klimesch, 1999, for reviews). These mixed findings might reflect a complex, task-specific, non-linear relationship between age and slow frequency activity, as is seen for amyloid load, with increased slow frequency and decreased faster frequency amplitudes appearing with more severe cognitive decline (Benwell et al., 2020).

1.2 The Current Study

The present study utilised the behavioural and eye-tracking methods used by Crawford and Higham (2016) in addition to measurements of resting state EEG with young and older adults. Resting state EEG has proven to be insightful for measuring large-scale organization of the human brain (Vlahou et al., 2014), and represents a baseline *default* activity that is suitable for establishing relationships with human behavior (Raichle, & Snyder, 2007).

Based on the literature summarized above, we hypothesised that relative to young adults, older adults would exhibit a slowing of alpha peak frequency and a reduction in alpha power alongside an increase in delta, theta and beta power. We hypothesized that higher cognitive performance and performance at eye tracking tasks would be related to increased alpha power and higher alpha peak frequency (c.f. Clark et al., 2004), with age differences in these tasks corresponding to age differences in EEG. We also hypothesized that increased slow wave power (delta and theta power) would correspond to higher cognitive performance in older adults (Finnigan and Robertson, 2011). Our measures of beta power were more exploratory: To our knowledge, the three-way combination of age, beta power and cognition has not been explored in the literature, and mixed results exist on the relationship between age and beta power, and on the relationship between beta power and cognition. Crucially, our data were able to evaluate if young and older adults showed *different* relationships between EEG and cognitive performance. Literature in this area is particularly limited; based on MEG research by Vlahou et. al (2014) we expected to find delta and theta power related to cognitive performance in older adults but not young adults.

2. Method

2.1 Participants

Data were collected from 88 participants, 2 participants were excluded (one due to a history of alcohol abuse, one due to hearing impairment which interfered with data collection) leaving 86 participants with behavioral data. Eleven participants were removed due to incomplete or excessively noisy EEG data. Therefore, the final sample consisted of 75 participants who had complete EEG and behavioral data, 31 young adults (aged 18–30 years old, M= 23.96, SD=4.52, 21 females, 10 males), and 44 older adults (aged 61–90 years old, M=71.47, SD=6.49, 28 females, 16 males). All participants were right-handed, native English speakers with, normal or corrected hearing and vision, no reported learning difficulties, no history of mental disorder, brain injury, neurological disorder, loss of consciousness for more than five minutes, or a history of alcohol or drug abuse within the last 12 months and were not taking any kind of mood-altering prescribed medication. Participants were recruited via the Nottingham Trent University ageing panel and paid participant panels. All participants were given £20 shopping vouchers for their participation. Ethical approval was obtained from the NHS.

2.2 Procedure

The following tests were administered first with duration reported in brackets: Digit span (5 mins), Spatial span (5 mins), Word Fluency (5 mins), and the Hopkins Verbal Learning Test Revised (HVLT-R; 5 mins). This was followed by the EEG set up and recording the resting state EEG (45 mins). Participants were then given a short 5 mins break. The Eye-tracking tasks were then completed (25 mins) followed by the Trail Making task (5 mins), and NART (5 mins). This completed the testing for the younger adults (~120 minutes in total). The older adults then had a 10 mins break and then the final tasks were administered: ADAS-COG, MMSE, and then GDS. The testing session for older adults took approximately 150 minutes in total.

2.3 Neuropsychological assessment

2.3.1 Verbal and spatial working memory

All participants completed digit span (Wechsler, 1997a; scored on 16 trials each for forward and backward), spatial span (Wechsler, 1997b; scored on 16 trials each for forward and backward) and Hopkins Verbal Learning Test Revised (Benedict, Schretlen, Groninger, & Brandit, 1998), scored out of 12, (words remembered minus related words not on the list).

2.3.2 Premorbid IQ

All participants completed the National adult reading test (NART; Nelson, 1982; number of errors recorded), verbal fluency (Storandt et al., 1984; number of words), and the trail making task (Reitan, 1958; time taken to complete task parts A and B recorded in seconds).

2.3.3 Dementia and Depression

Older adults also completed ADAS-COG (Dahalke et al., 1992; Rosen et al., 1984); Mini mental state exam (MMSE; Molley, Alemayehu & Roberts, 1991; score out of 30) and the Geriatric depression scale (GDS; Yesavage et al., 1983).

2.4 Eye-tracking

An Eyelink 1000 SR eye tracker was used with a 1000 Hz sampling rate. A six-point calibration and validation was performed before the start of each condition. Calibration was not always successful with older adults and analyses represent data from 28 older adults. The stimuli were displayed on a PC with a 40cm x 30cm, 1280 x 720 pixels screen resolution. The eye-tracking procedure was replicated from Crawford and Higham (2005; 2016). Seven conditions were used (see Figure 1): Prosaccade (24 trials: gap, 24 trials: overlap), anti-Saccade (24 trials: gap, 24 trials: overlap) and go/no go (No Go: 10 trials, Go Left: 5 trials, Go Right: 5 trials). Each condition was proceeded by 4–6 practice trials. The target dot was 15 pixels in diameter (.59cm).

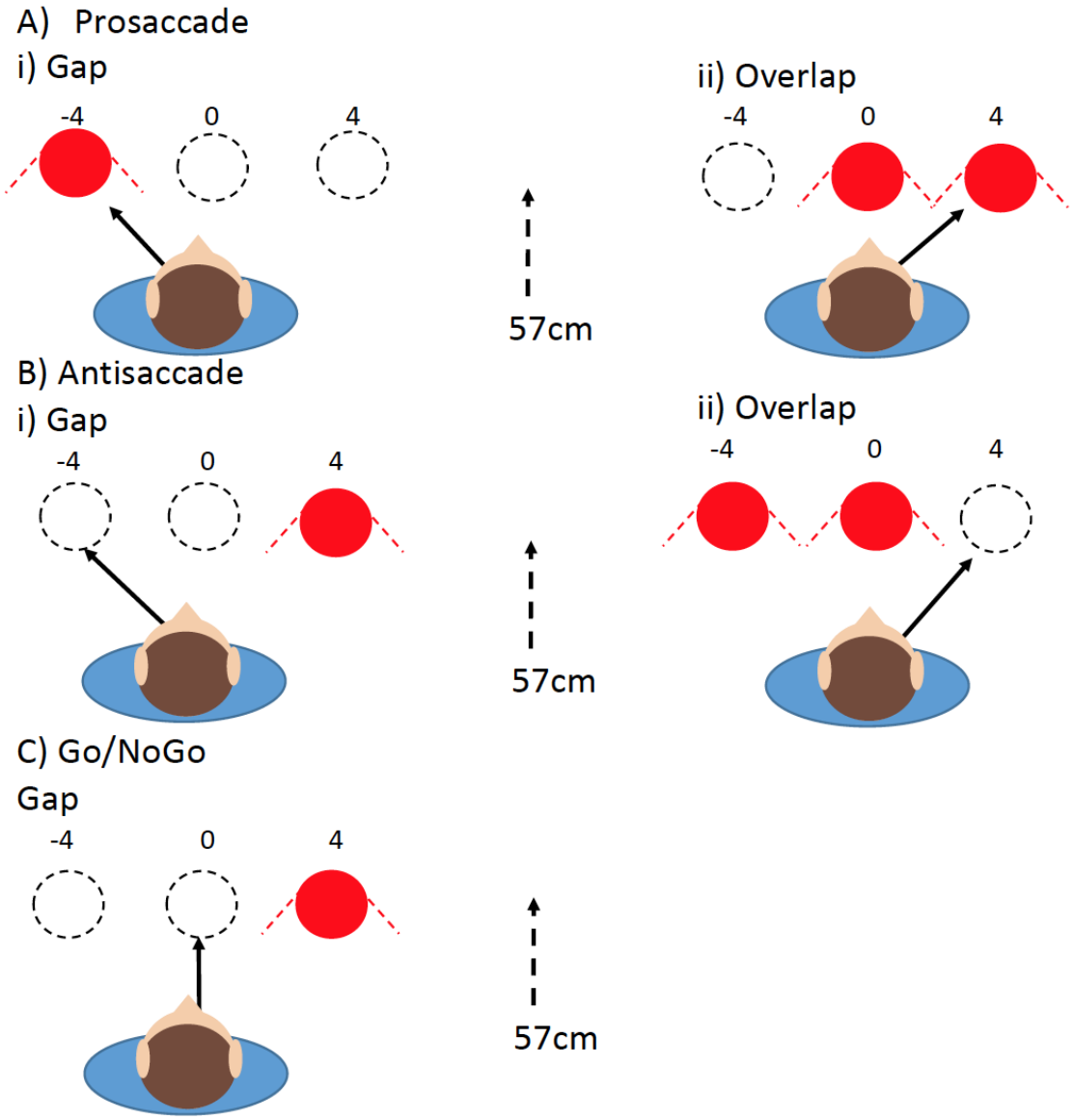


Figure 1. Shows a top down view of a participant seated 57cm from the screen with the red target dot presented at -4/4 degrees, the arrows indicate direction of gaze. Panel A: (i) shows the Prosaccade gap task in which the participant is required to make a saccade to the red target which appears on either the left or the right. The central dot was displayed for 1000ms, the target then appeared to the left or the right 200ms after the central fixation point disappeared and was displayed for 2000ms, ii) the overlap task was the same but the central fixation point remained on screen when the target appeared meaning that both target and central fixation point were on the screen simultaneously for 200ms. Panel B: (i) The antisaccade gap was the same as the prosaccade gap task with the important difference that the task required the participant to look in the opposite direction to where the target appeared, as shown in the figure the target appears on the right so the participant looks left, ii) the antisaccade overlap task is the same but the central fixation point remained on screen when the target appeared. Panel C: In both the Go and No-Go tasks the central fixation duration was 1000ms, there

was then a 200ms gap followed by the target presentation for a duration of 700ms. For the go task (not shown) if the target appears on the left the participant looks at the target as in prosaccade trials, for the No-Go trials (shown) if the target appears on the right, the participant must ignore it and maintain their gaze on the fixation point (two versions of the Go/No-Go task were used with left and right instructions reversed).

2.5 EEG

Resting state EEG was recorded for two conditions - 5 minutes with the participants' eyes open and then 5 minutes with their eyes closed. For each condition, participants completed 2.5 minutes and then had a break followed by another 2.5-minute block. During the eyes open condition, the participant looked at a white fixation cross on a grey screen. A Biosemi ActiveTwo system (Amsterdam, The Netherlands) and electrode cap were used to record continuous EEG from 128 channels, based on the 5% (10-5) system (sampling rate=2048Hz).

Signal processing of EEG data was performed using Curry 7.12 software. Offline data were filtered (1–35Hz) and corrected using a constant baseline. Eye-movement artefacts were reduced using PCA methods. Epochs of 2 seconds duration were created and auto-detection was used to identify residual artefact (above/below 60 microVolts). Any remaining artefact was removed manually. An average reference was then applied, and spectral analysis (non-log transformed) used to extract power for each band: delta (1-4Hz), theta (4-8Hz), alpha (8-12Hz), beta (12-20Hz) in each 2 second epoch. Average power across all epochs for each frequency band was then calculated.

Data were averaged across electrodes into 14 regions: left frontal (C25, C26, C27, C28, C29, C30, C31, C32) right frontal (C3, C4, C5, C6, C7, C9, C10, C11, C12, C13, C14, C15, C17), midline frontal (C17, C18, C19, C20, C21, C22), left occipital (A10, A11, A12, A13, A14, A15, A16, A17), right occipital (A26, A27, A28, A29, A30), midline occipital (A21, A22, A23, A24, A25), left temporal (D22, D23, D24, D25), right temporal (B25, B26, B27, B28), left parietal (A5, A6, A7, A8, A9), right parietal (B3, B4, B5, B6), midline parietal (A3, A4), left central (D28, D27, D26, D29, D30, D31, D32), right central (B19, B20, B21, B22, B23, B24) and midline central (A1, A2).

3. Results

The sample size used in each analysis is outlined in the relevant section, where appropriate the Bonferroni correction was used for multiple comparisons and unless stated otherwise, unadjusted *p*-values are reported. Results were analysed using SPSS V.24.0. Table 1 shows the descriptive statistics for the neuropsychological tests and the results of t-tests comparing each age group. Performance on the verbal working memory tasks was similar across groups. Older adults were slower than younger

adults to complete the trail making task parts A and B. Younger adults made twice as many errors than did older adults on the NART. There were no other statistically significant differences between groups. Younger adults performed slightly better on both the forward and backward spatial span tasks. All older participants showed intact cognitive ability, scoring over 22 on the MMSE (c.f. Monroe & Carter, 2012) or less than 13 on the ADAS-COG (Monllau et al., 2007). No geriatric depression was found in participants, who all scored less than 7 out of 30 where scores lower than 10 indicate the absence of depression (Yesavage et al., 1983).

Table 1.

Descriptive Statistics and t-tests for Each of the Cognitive Tests

	Younger			Older			Age Difference		
	Mean	SD	N	Mean	SD	N	*t*	*df*	*p**
Trail making part A	21.46	5.798	36	32.89	14.394	50	-5.07	69	.001
Trail making part B	42.92	11.446	36	62.45	27.112	50	-4.56	70	.001
NART errors	22.17	7.272	36	11.32	5.589	50	7.821	84	.001
Word fluency	21.69	6.201	36	21.82	6.727	50	-0.088	84	.930
Hopkins verbal learning	11.31	2.786	36	10.82	1.307	51	1.08	85	.283
Digit span forward	11.17	2.513	36	10.68	2.535	50	0.882	84	.381
Digit span backward	8.94	2.229	36	8.56	2.612	50	0.715	84	.477
Spatial span forward	8.92**	1.962	36	6.51	1.938	49	5.627	83	.001
spatial span backward	8.47	1.762	34	6.35	2.006	49	4.981	81	.001
MMSE				28.57	1.85	49			
ADAS				8.00	3.89	50			
GDS				1.31	1.50	49			

**Significance unchanged following Bonferroni adjustment (unadjusted reported)*

***Young adults' forwards spatial span correlated with antisaccade (gap condition) accuracy, $r(33) = .599$, $p < .001$ (unadjusted) there were no other correlations with eyetracking measures after accounting for multiple comparisons.*

3.1 Eyetracking Analysis

Saccade reports were generated with Data Viewer by EyeLink (https://www.sr-research.com/data-viewer/) using the default settings which reported all saccades occurring within each trial. The accuracy of a saccade was determined by establishing if the starting position of the saccade or the ending position of the saccade was closer to the target position (defined as the target itself for prosaccades and the mirror opposite position of the target for antisaccades). Saccade accuracy was then defined as the proportion of all saccades in the correct direction following target onset and up to 1200ms beyond target onset (c.f. Smyrnis, 2008), small saccades less than 1.5 degrees in amplitude were excluded as well as anticipatory saccades occurring within 80ms of target onset. Correct responses for nogo trials were recorded if no saccades were made during the trial.[1] Saccade response times were calculated for correct saccades and were defined as the mean response time in the interval between 80–1200 ms post target onset.

Initially, to compare the prosaccade and antisaccade tasks, a 2 (Age; young older) x 2 (Saccade task; antisaccade, prosaccade) x 2 (Target onset condition; overlap, gap) ANOVA was conducted on the response times for correct responses (see Figure 2 for means). The natural logarithm of response times (in milliseconds) was used to avoid spurious interactions derived from general slowing in older adults (Verhaeghen, 2011). Older adults were slower than young adults $F(1,59) = 12.91$, $p < .001$, $\eta_p^2 = .18$, responses to the antisaccade task were slower than responses to the prosaccade task, $F(1, 59) = 302.67$, $p < .001$, $\eta_p^2 = .84$, and having the target appear whilst the fixation dot remained on screen in the overlap condition resulted in slower responses than in the gap condition when the fixation dot disappeared before target onset, $F(1, 59) = 393.73$, $p < .001$, $\eta_p^2 = .87$. An interaction between saccade task and target onset condition showed that the gap condition increased the speed of responses relative to the overlap condition more for prosaccades than for antisaccades, $F(1, 59) = 25.30$, $p < .001$, $\eta_p^2 = .30$. The remaining interactions were non-significant (ps > .10).

The same factors were used in a separate ANOVA with accuracy as the dependent variable (see Figure 2 for means). Older adults were less accurate than young adults, $F(1, 59) = 4.78$, $p = .033$, $\eta_p^2 = .08$. The antisaccade task resulted in lower accuracy than the saccade task, $F(1, 59) = 29.84$, $p < .001$, $\eta_p^2 = .34$. In contrast to the response time data, responses were more accurate with the overlap than with the gap target onset condition, $F(1, 59) = 9.45$, $p = .003$, $\eta_p^2 = .14$, suggesting speed accuracy trade-offs. There were no interactions (Fs < 1, see Figure 2 for means).

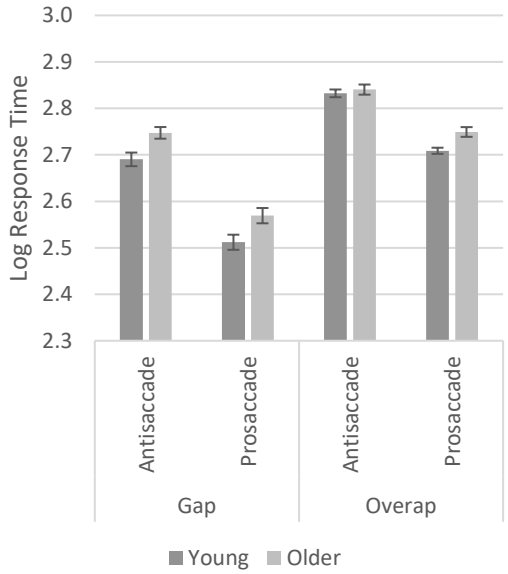
[1] Trials with no saccades and trials containing multiple saccades were weighted equally. For example, if five erroneous saccades were produced in one trial, this would count towards the average to the same extent as a trial with no saccades.

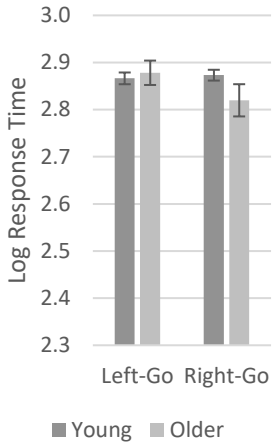
Incorrect response times were analysed for prosaccades and for antisaccades (see Figure 2 for means). Older adults' incorrect responses were faster than young adults' incorrect responses, $F(1, 56) = 4.03$, $p = .0496$, $\eta_p^2 = .07$, incorrect responses to the antisaccade task were faster than incorrect responses to the prosaccade task, $F(1, 56) = 81.37$, $p < .001$, $\eta_p^2 = .59$, and incorrect responses were faster for the gap target onset condition than for the overlap target onset condition, $F(1, 56) = 9.56$, $p = .003$, $\eta_p^2 = .15$. There was an interaction between saccade task and target onset condition, $F(1, 56) = 7.81$, $p = .007$, $\eta_p^2 = .12$, such that the difference in incorrect response times for gap and overlap conditions was similar for prosaccades, but for antisaccades the gap responses were faster than the overlap responses. The remaining interactions were non-significant (ps > .10).

The go/nogo saccade data were analysed using a 2 (Age; young older) x 2(Go direction; left, right) ANOVA on correct response times. Only go trials were used as nogo trials did not require saccades and as above, logarithms were utilised (see Figure 2 for means). There was no main effect of age, $F < 1$, or direction, $F(1, 59) = 3.00$, $p = .089$, $\eta_p^2 = .05$. An interaction showed that older adults were slower for the go-right condition than the go-left condition, whilst young adults performed similarly in both conditions, $F(1, 59) = 4.91$, $p = .031$, $\eta_p^2 = .08$.

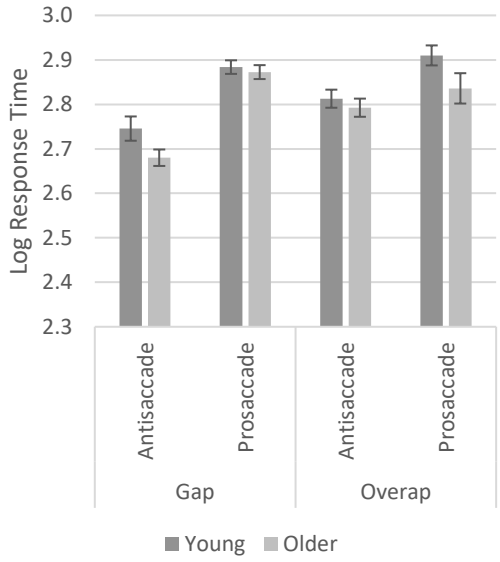
For go/nogo accuracy, a 2 (Age; young older) x 2 (Go direction; left, right) x 2 (trial type: go, nogo) ANOVA was conducted on the accuracy data (see Figure 1 for means). Older adults were less accurate than young adults, $F(1, 59) = 9.18$, $p = .004$, $\eta_p^2 = .14$. There was no main effect of Go direction, $F(1, 59) = 2.18$, $p = .145$, $\eta_p^2 = .04$, or trial type, $F < 1$. There were no interactions (ps > .12).

Correct Response Times

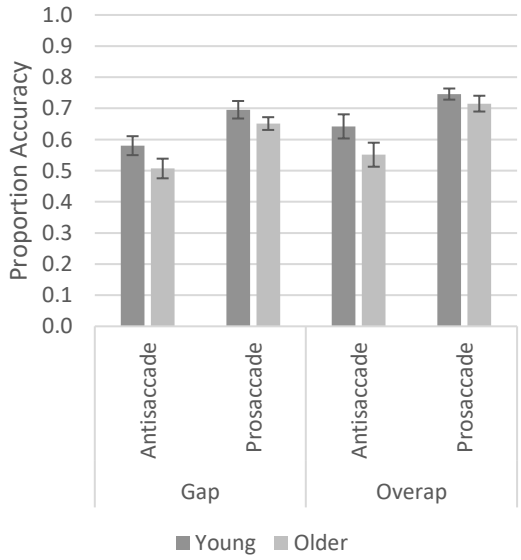




Incorrect Response Times



Accuracy



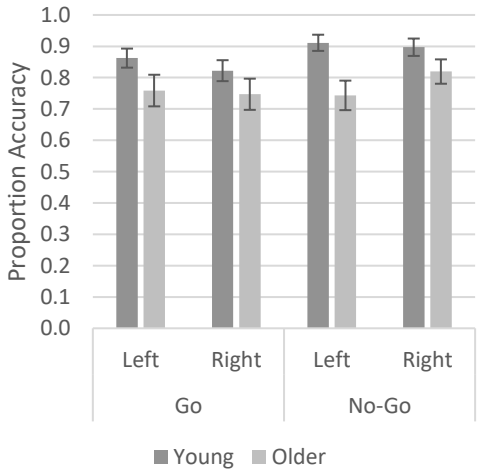


Figure 2. Top: Response times for correct responses for antisaccade and prosaccade task (left) and for go/nogo task (right, go trials only). Middle: Response times for incorrect responses for antisaccade and prosaccade task. Bottom: Accuracy for antisaccade task and prosaccade task (left) and for go/nogo task (right). Error bars are ± 1 *SE*.

3.2 EEG Power

Separate ANOVAs were conducted for each EEG frequency band with the following factors: Age Group (young, older) between participants, Condition (eyes open, eyes closed), Site (frontal, parietal, temporal, central, occipital) and Hemisphere (Left, Right) within participants. The Greenhouse-Geisser correction was applied to degrees of freedom where assumptions of sphericity were violated.

3.2.1 Delta and Theta Power

Delta and theta EEG power showed no main effects of age, Fs < 1, and no interactions with age (see Appendix Tables A1 and A2 for analyses and means respectively).

3.2.2 Beta Power

For the ANOVA with the dependent variable beta activity (see Figure 3 for heatmap and Figure 4 for means), older adults had increased beta activity compared to younger adults, $F(1,73) = 4.30$, $p = .042$, $\eta_p^2 = .06$. There was also a significant effect of Site, $F(2.95, 215.48) = 26.73$, $p < .001$, $\eta_p^2 = .27$. Pairwise comparisons with Bonferroni correction indicated that beta activity was highest over the occipital site compared to the frontal, central and parietal sites (ps < .018) but not higher than the second highest activity in the temporal site ($p > 1$), the temporal activity was higher than the central and the parietal activity (ps < .021) but not significantly higher than the third highest activity at the frontal site ($p = .239$), the frontal activity was higher than the central activity (p <.001) but not the parietal activity (p >1). There was no main effect of Condition or Hemisphere, Fs <1. There was an interaction between Condition and Site $F(2.48, 181.63) = 17.61$, $p < .001$, $\eta_p^2 = .19$, with frontal and temporal sites decreasing in power from eyes open to eyes closed whilst central, parietal and occipital power increased from eyes open to eyes closed. There was an interaction between Condition and Hemisphere $F(1,73)= 8.88$, $p=.004$, $\eta_p^2 =.11$, for the left hemisphere, power decreased from eyes open to eyes closed whilst for the right hemisphere, power increased from eyes open to eyes closed. There was also a significant three-way interaction between Condition, Site and Hemisphere $F(2.66, 194.44) = 4.64$, $p = .001$, $\eta_p^2 = .06$, which was predominantly evident in the temporal site where power decreased from eyes open to eyes closed but to a greater extent in the left hemisphere compared to the right. No other effects or interactions were significant (ps > .251).

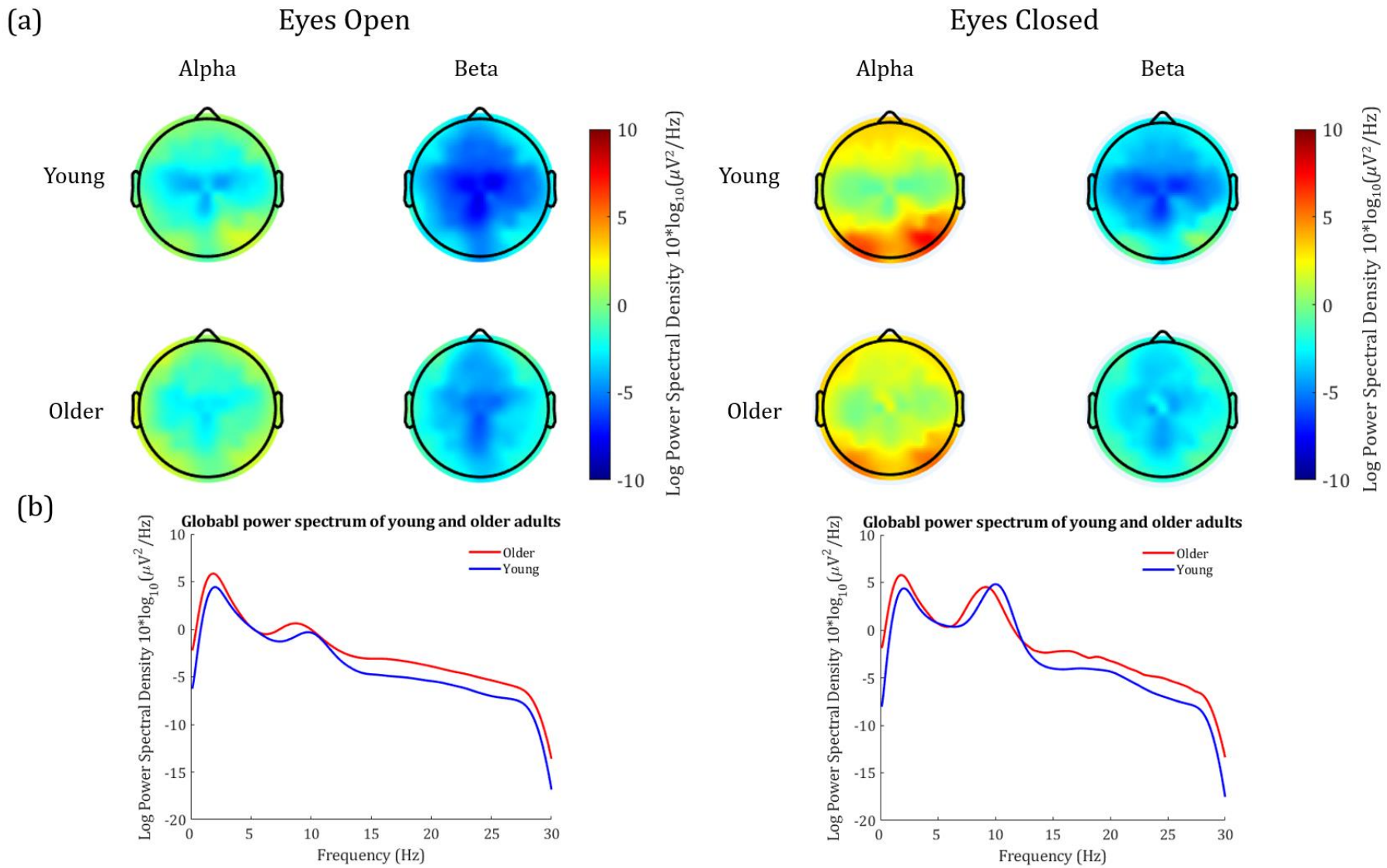

(a)
Eyes Open
Eyes Closed
Alpha
Beta
Young
Older
10
5
0
-5
-10
Log Power Spectral Density 10*log10(μV²/Hz)
(b)
Globabl power spectrum of young and older adults
Older
Young
Log Power Spectral Density 10*log10(μV²/Hz)
Frequency (Hz)
0
5
10
15
20
25
30
-20
-15

Figure 3. Average power spectral plots for young and older adults for eyes open and eyes closed resting-state EEG. (a) Topographic heatmaps showing alpha and beta power for young and older adults. (b) Power spectral density plot of resting-state EEG for young and older adults averaged over all electrodes.

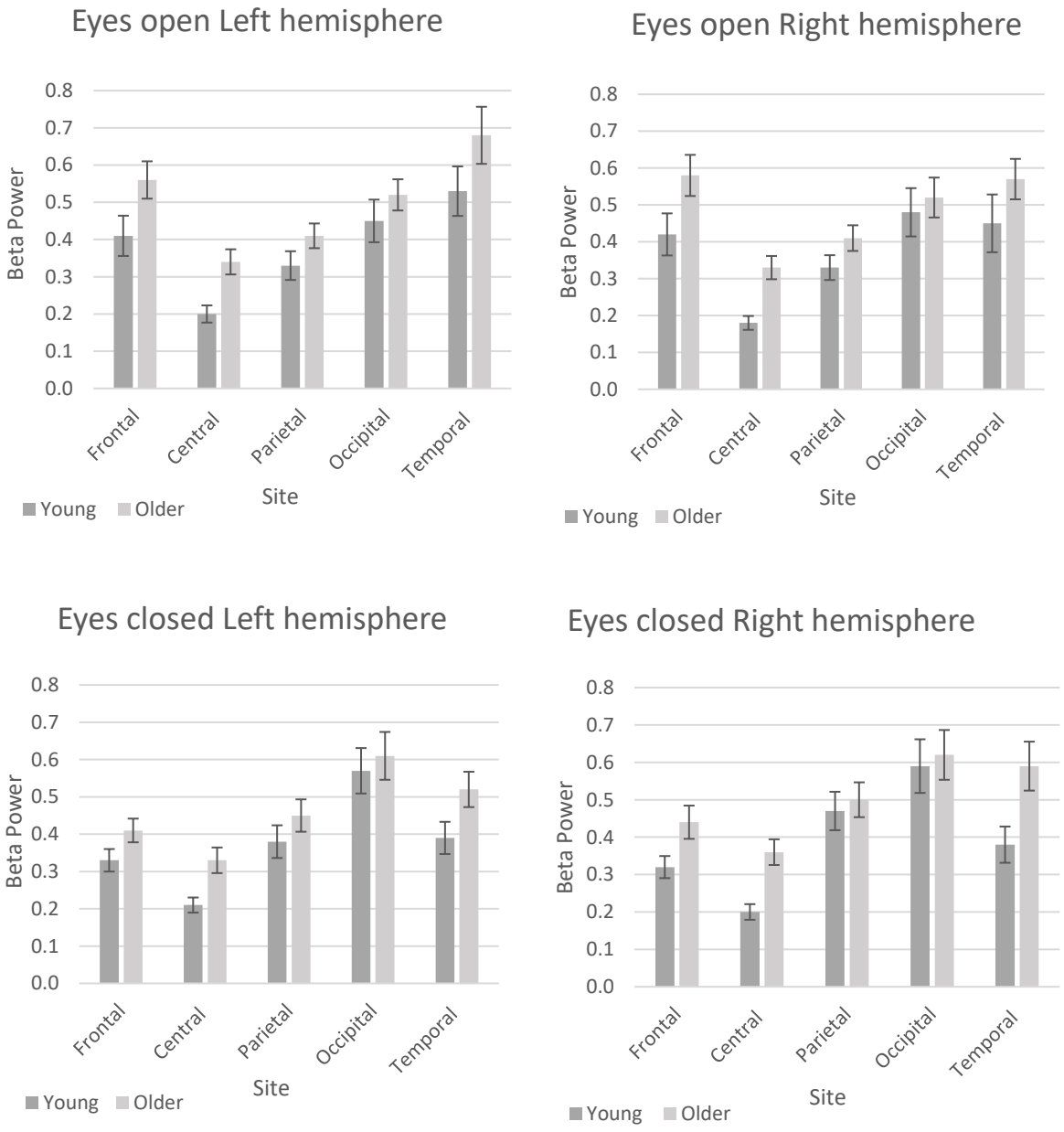


Figure 4. Beta power for young and older adults across frontal, central, parietal, occipital and temporal sites and across left and right hemispheres for eyes open and eyes closed conditions. Error bars are ± 1 *SE*.

3.2.3 Alpha Power

For the ANOVA with the dependent variable alpha power (see Figure 3 for heatmap and Figure 5 for means), there was no main effect of Age Group, $F < 1$. Alpha power increased in the eyes closed condition compared to the eyes open condition, $F(1,73) = 66.13$, $p < .001$, $\eta_p^2 = .48$. There was a main effect of Site $F(1.41, 102.90) = 52.80$, $p < .001$, $\eta_p^2 = .42$. Pairwise comparisons showed that that alpha power was significantly different for all comparisons between regions (ps < .001) except the comparison between frontal and temporal regions (p >1). The ordinal power at each region was occipital > parietal > frontal > temporal > central. Alpha power was greater in the right hemisphere compared to the left hemisphere, $F(1,73) = 22.80$, $p < .001$, $\eta_p^2 = .24$. There was an interaction between Condition and Site, $F(1.26, 91.61) = 37.57$, $p < .001$, $\eta_p^2 = .34$, with the effects of Site generally being more extreme in the eyes closed condition compared to the eyes open condition. There was an interaction between Condition and Hemisphere, $F(1, 73) = 18.66$, $p < .001$, $\eta_p^2 = .20$, with the effects of Hemisphere more extreme for the eyes closed condition than for the eyes open condition. There was an interaction between Site and Hemisphere, $F(1.93, 141.16) = 17.33$, $p < .001$, $\eta_p^2 = .19$, with similar power across hemispheres for all Sites apart from the parietal area which showed greater power in the right hemisphere. A triple interaction was present between Age Group, Site and Hemisphere, $F(1.93, 141.16) = 5.09$, $p = .008$, $\eta_p^2 = .07$, such that the asymmetrical parietal power evidenced in the Site by Hemisphere interaction above was largely driven by young adults, with older adults showing less asymmetrical activity. Another triple interaction was present between Condition, Site and Hemisphere, $F(1.88, 137.37) = 17.77$, $p < .001$, $\eta_p^2 = .20$, the asymmetrical parietal power was more evident for the eyes closed than for the eyes open condition. Finally, the quadruple interaction was also present between Age Group, Condition, Site and Hemisphere, $F(1.88, 137.37) = 4.65$, $p = .013$, $\eta_p^2 = .06$, which was driven by asymmetry of parietal power only, just for young adults and predominantly in the eyes closed condition. The remaining interactions were non-significant (ps > .059).

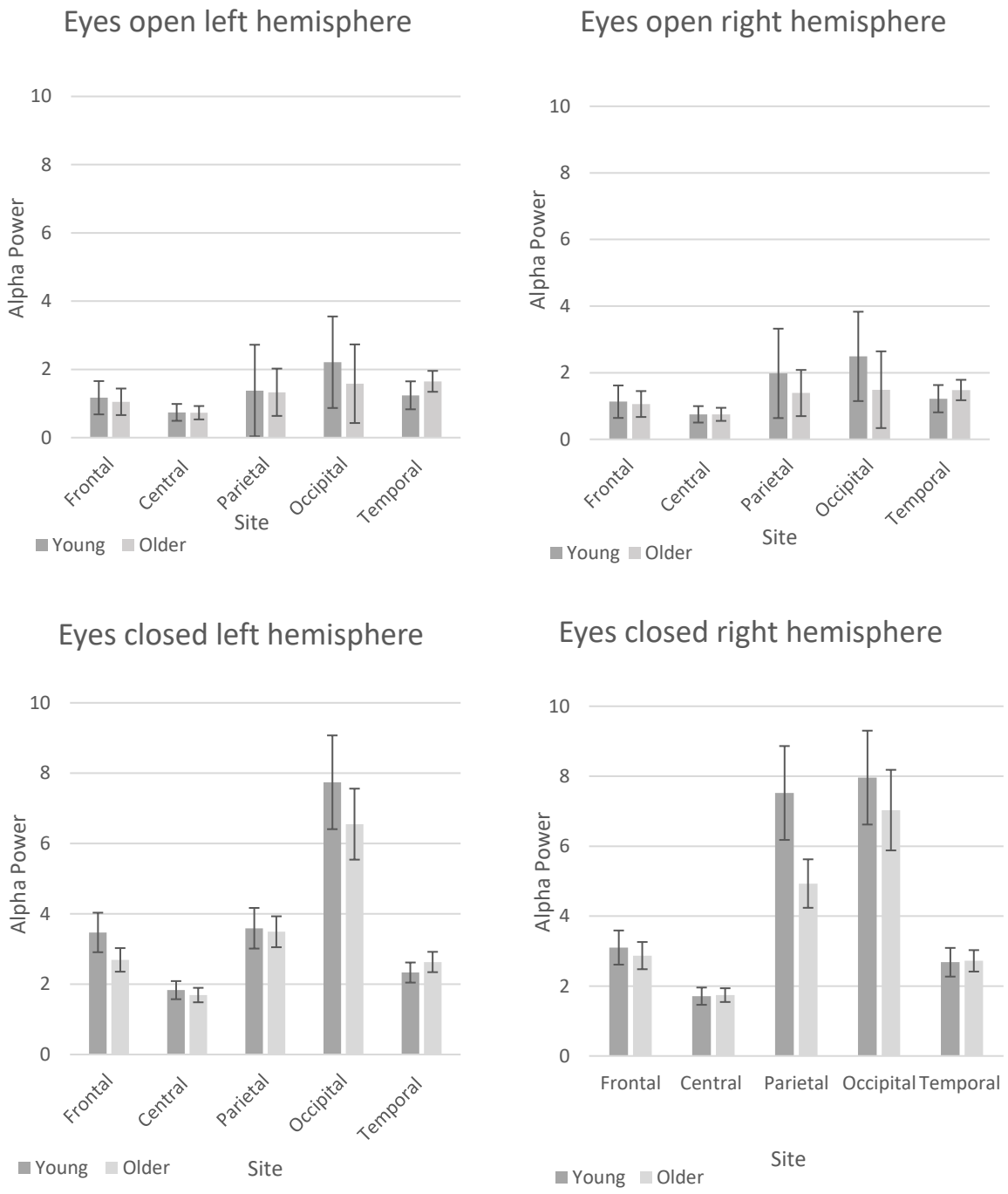


Figure 5. Alpha power for young and older adults across frontal, central, parietal, occipital and temporal sites and across left and right hemispheres for eyes open and eyes closed conditions. Error bars are ± 1 *SE*.

3.3 Alpha Peak Frequency

The same Age Group x Condition x Site x Hemisphere ANOVA structure was used for the dependent variable alpha peak frequency (see Figure 3 for global power spectrum and Figure 6 for means). Older adults displayed reduced alpha peak frequency compared to younger adults, $F(1,73)=5.56$, $p=.021$, $\eta_p^2 =.071$. Alpha peak frequency was higher for the eyes closed compared to the eyes open condition, $F(1,73)=4.55$, $p=.036$, $\eta_p^2 = .06$. There was a main effect of Site, $F(2.82,205.91) = 11.37$, $p<.001$, $\eta_p^2 = .14$. Pairwise comparisons showed that the highest alpha peak frequency over the parietal region was significantly higher than the frontal ($p <.001$) and central regions ($p <.001$) but not significantly higher than the second highest frequency over the occipital region ($p = .253$). The occipital region was significantly higher than the frontal region ($p = .021$), but not the third highest frequency over the temporal region ($p > 1$). The temporal region was significantly higher than the frontal region only ($p = .021$). Alpha peak frequency was higher in the right hemisphere than in the left hemisphere, $F(1,73) = 6.66$, $p=.012$, $\eta_p^2 = .084$. There was an interaction between Condition and Site $F(2.79,203.75)=2.74$, $p = 0.048$, $\eta_p^2 =.04$, with the effect of Site more extreme for the eyes open condition than for the eyes closed condition. There was an interaction between Condition and Hemisphere $F(1,73) = 6.05$, $p= .016$, $\eta_p^2 =.08$, with the effects of Hemisphere more extreme for the eyes open condition than for the eyes closed condition. There was also a quadruple interaction between Age Group, Condition, Site and Hemisphere, $F(3.24,236.89) = 2.87$, $p = .033$, $\eta_p^2 =.04$: For young adults only, for temporal regions only, and for eyes closed only, the peak frequency was higher in the left hemisphere than in the right hemisphere, whilst every other condition and site showed a greater peak frequency in the right hemisphere compared to the left hemisphere. No other interactions were significant ($ps > .189$).

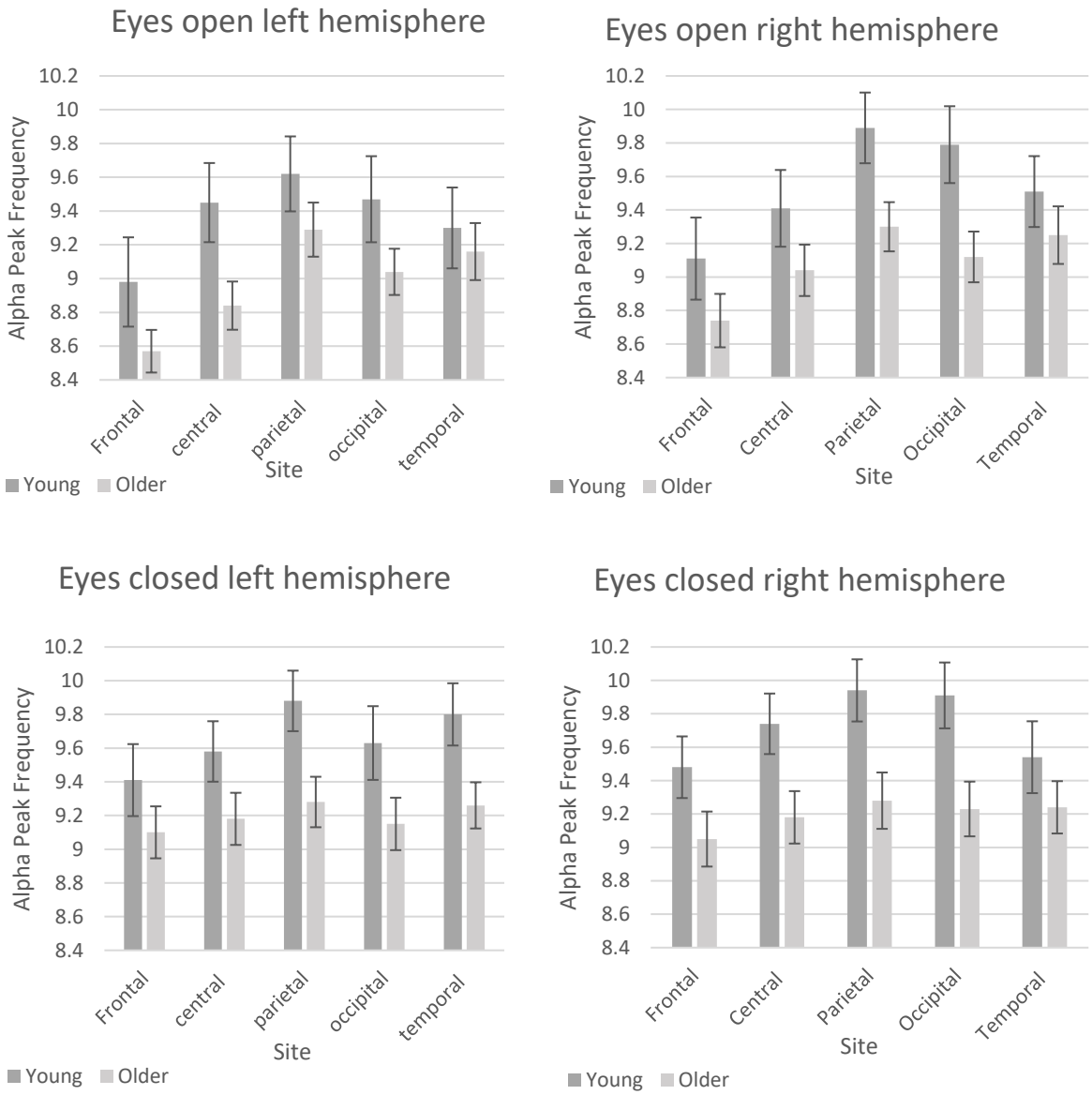


Figure 6. Alpha peak frequency for young and older adults across frontal, central, parietal, occipital and temporal sites and across left and right hemispheres for eyes open and eyes closed conditions. Error bars are ± 1 *SE*.

3.4 Age interactions with EEG, Cognition and Eye-Movement Analyses

A series of analyses were conducted to establish if cognitive abilities and eye-tracking were related to EEG activity. Single EEG measures were constructed as outcome variables for a hierarchical regression with cognitive/eye-tracking variables as predictors in the first stage and age as a predictor in the second stage. This would establish if there were any relations between cognition and EEG and if they were still present after accounting for age. Only significant effects are reported for brevity.

3.4.1 Beta Power

As beta power differed significantly between age groups, this was used to generate a single EEG measure. All beta power values were collapsed into a single average (20 data sets: left hemisphere/right hemisphere x eyes closed/eyes open x 5 Sites; Cronbach alpha = .95) for comparison with other measures.

3.4.1.1 Visual and non-visual working memory

Forwards and backwards digit span and forwards and backwards spatial span were entered as four predictors into a hierarchical multiple regression to predict total beta power, with participant age added at the second stage. No overall effects were significant. Only one significant predictor was present (forwards spatial span, standardised beta = -.322, p = .029) in the first stage only.

3.4.1.2 Eye movement accuracy

The eye-tracking accuracy from the prosaccade, antisaccade, go-left, and go-right tasks (using the conditions with a gap between fixation and target onset) were entered into a similar hierarchical multiple regression to predict total beta power, with participant age added at the second stage. No effects were significant.

3.4.1.3 Eye movement response times

The corresponding log-transformed response time eye-tracking measures (prosaccade, antisaccade, go-left, and go-right) were then used to predict total beta power in a similar hierarchical regression with age entered as an additional predictor at the second stage. A significant proportion of the total beta power variance was accounted for in the first stage, R^2_{adj} = .192, F(4, 45) = 3.91, p = .008, and in the second stage R^2_{adj} = .198, F(5, 44) = 3.42, p = .011, but adding age as a predictor did not significantly improve the second model relative to the first, F(1, 44) = 1.32, p = .257. Table 2 shows that prosaccade response time was longer as total beta power increased in both models and that go-left response time was longer as total beta power decreased, once age was entered into the second stage.

Table 2.

Coefficients for the Models with the Eye-Tracking Response Time Measures as Predictors of Beta Power

			Unstandardized Coefficients		Standardized Coefficients		
Condition			*B*	Std. Error	Beta	*t*	*p*
	Model 1	(Constant)	-0.01	1.279		-0.004	0.997
		Antisaccade gap	0.241	0.33	0.097	0.73	0.469
		No go left (go)	-0.633	0.332	-0.334	-1.907	0.063
		No go right (go)	-0.077	0.267	-0.051	-0.287	0.775
		Prosaccade gap	0.724	0.315	0.323	2.298	0.026
	Model 2	(Constant)	0.464	1.339		0.346	0.731
		Antisaccade gap	0.119	0.346	0.048	0.343	0.733
		No go left (go)	-0.762	0.349	-0.402	-2.182	0.035
		No go right (go)	0.018	0.279	0.012	0.066	0.947
		Prosaccade gap	0.683	0.316	0.305	2.16	0.036
		Age	0.002	0.001	0.17	1.147	0.257

The prosaccade response times were analysed further as they were significantly predicted by beta power and also because they are distinct in that they represent the fastest responses of all the eye-tracking tasks (minimal speed/accuracy trade-offs). To explore whether the relationship between beta power and prosaccade response times depended on age, a hierarchical regression model was constructed with an interaction term. The variables age of participant and total beta power were centralised by subtracting them from their own means and then multiplied together to produce an interaction variable age x total beta (Warner, 2008). A two-stage hierarchical regression was conducted using the centralised age and centralised total beta power measures in the first stage as predictors of the log transformed prosaccade response time. At the second stage the age x total beta power interaction variable was entered as an additional predictor. Age and beta power significantly predicted prosaccade response times in the first model, R^2_{adj} = .127, $F(2, 56) = 5.21$, $p = .008$, rising to, R^2_{adj} = .196, $F(3, 55) = 5.72$, $p = .019$ in the second model with the .081 R^2 change showing a significant increase in the variability explained by the second model which included the interaction term, $F(1, 55) = 5.84$, $p = .019$. This indicated that the relationship between beta power and prosaccade response time depended on age. Table 3 shows that all predictors were significant in both

models. Follow up correlation analyses showed that for young adults, higher total beta power corresponded to slower prosaccade responses, $r(29) = .519$, $p = .004$, whereas for older adults, there was no relation between total beta power and prosaccade responses, $r(32) = -.027$, $p = .884$, these correlations were also significantly different from one another using Fisher's r-to-z transformation and a two-tailed null hypothesis test, $p = .026$.

Table 3.

Beta Coefficients for the Models with Predictors Beta Power and Age Predicting Prosaccade RT

Condition			Unstandardized Coefficients		Standardized Coefficients		
			B	Std. Error	Beta	*t*	*p*
	Model 1	(Constant)	2.542	0.012		203.7	0
		Age	0.001	0.001	0.263	2.107	0.04
		Beta	0.123	0.06	0.254	2.042	0.046
	Model 2	(Constant)	2.547	0.012		209.42	0
		Age	0.001	0	0.258	2.159	0.035
		Beta	0.122	0.058	0.252	2.109	0.039
		Age by Beta	-0.006	0.002	-0.284	-2.416	0.019

3.4.2 Alpha Parietal Power

Although there was no main effect of age on alpha power in the EEG analyses there was an interaction involving age; from Figure 5 it can be seen that the 4 way interaction was driven by parietal asymmetry for young but not for older adults during eyes closed resting state. A new variable was constructed by subtracting the left from the right parietal power in the eyes closed condition. This new variable significantly differed across age, $t(37.29) = 2.27$, $p = .029$, and was used to compare performance in cognitive and eye-tracking tasks similar to the beta analyses above. Using this EEG measure as the outcome variable the same set of regressions were conducted as in the section above. There were no significant predictions by cognitive or eye-tracking measures in any of the models apart from forwards spatial span (standardised beta = .314, $p = .032$) in the first stage only of the visual and non-visual working memory model.

3.4.3 Alpha Peak Frequency

As alpha peak frequency differed significantly across age, this was also investigated further. Initially, we collapsed all alpha peak frequency measurements into a single average (20 data sets: left hemisphere/right hemisphere x eyes closed/eyes open x 5 Sites; Cronbach alpha = .96) for comparison to other measures. Analyses were repeated as outlined above. There were no significant predictions by cognitive or eye-tracking measures in any of the models.

3.5 Direct Replications

Correlation analyses (see Table 4) were conducted to attempt to replicate the findings of Finnigan and Robertson (2011) who examined theta power at Fz and Pz and alpha peak frequency during eyes closed resting EEG and Clark et al. (2004) who found alpha peak frequency was linked to working memory. Unlike Finnigan and Robertson (2011), we did not find a relationship between frontal theta and any of the cognitive tests. We did find that higher frontal alpha peak frequency in older adults corresponded to higher working memory span across several working memory measures (c.f. Clark et al. 2004), although this did not survive a Bonferroni correction for multiple tests.

Vlahou et al. (2014) found interactions with age and slow wave power in central and temporal regions when they were used to predict trail making task performance. Table 5 shows correlations between age and each of our cognitive measures for central and temporal eyes open EEG power in the delta and theta bands. No individual correlations were significant after correcting for multiple tests, however the difference in the correlations between young and older adults (using Fisher's *r* to *Z* transformation) was significant for trail making part B even after correcting for the 36 comparable comparisons in Table 5. These findings replicate Vlahou et al. (2014): For older adults, increased central delta power resulted in faster completion of the trail making test but the young adults showed a smaller relation in the opposite direction. Two-stage hierarchical regression models were used to predict trail making performance with age and slow wave power, using interaction terms in the second stage. The model predicting trail making B performance with age and central delta power entered at the first stage and the age x central delta power interaction term at the second stage showed a significant R^2 change when the interaction term was added, $F(1, 69) = 5.02$, $p = .028$. This is congruent with the significant differences found between the young and older adults' correlations outlined above. For comparable analyses using temporal delta power, central theta power or temporal theta power, the interactions terms did not significantly improve the models. There were also no improvements with interaction terms when predicting tail making part A.

Table 4.

Spearman Correlations Between Neuropsychological Tests, Theta Activity and Alpha peak Frequency at Frontal And Parietal Sites (Eyes Closed EEG)

	Young					Older				
	Alpha peak frequency		Theta			Alpha peak frequency		Theta		
	Frontal	Parietal	Frontal	Parietal	N	Frontal	Parietal	Frontal	Parietal	N
Trail making part A	0.026	-0.034	0.253	0.056	31	-0.248	-.310*	-0.036	0.072	44
Trail making part B	0.194	0.173	0.262	0.155	31	-0.179	-0.159	-0.006	0.108	44
NART	0.333	0.212	0.342	.406*	31	0.037	0.012	0.022	0.005	44
Word fluency	-0.1	-0.204	-0.147	-0.154	31	0.19	0.121	-0.111	-0.171	44
Hopkins verbal learning	0.203	0.245	0.06	0.02	31	0.01	0.098	-0.013	-0.024	44
Digit span forward	-.379*	-0.129	-0.228	-0.185	31	.367*	0.285	0.011	0.026	43
Digit span backward	-0.091	-0.058	-0.224	-0.228	31	.333*	0.22	-0.084	-0.063	43
Spatial span forward	0.065	0.052	0.033	-0.206	31	0.255	0.263	0.179	0.126	42
spatial span backward	-0.058	-0.087	-0.284	-0.134	30	.357*	0.303	0.204	0.186	42
MMSE					n/a	0.187	0.124	0.196	0.156	43
ADAS					n/a	-0.184	-0.192	0.087	0.144	44
GDS					n/a	-0.045	0.066	-0.125	0.07	42

*p<.05 but non-significant after correction for multiple tests

Table 5.

Spearman Correlations Between Neuropsychological Tests, Delta Power and Theta Power at Central and Temporal Sites (Eyes Open EEG)

	Young					Older					Fisher r-to-Z *p* value for young old correlation difference (two tailed)			
	Delta		Theta			Delta		Theta			Delta		Theta	
	Central	Temporal	Central	Temporal	N	Central	Temporal	Central	Temporal	N	Central	Temporal	Central	Temporal
Trail making part A	.136	.189	.070	-.010	31	-.183	-.124	-.219	-.153	44	.1902	.1971	.234	.5552
Trail making part B	.348	.350	.293	.187	31	-.436*	-.208	-.296	-.139	44	.0007**	.0188*	.0131*	.1802
NART	.219	.327	.183	.254	31	.029	-.073	.143	.019	44	.4295	.093	.865	.3271
Word fluency	-.046	-.142	.054	-.207	31	.184	.137	-.091	-.170	44	.3421	.4654	.5552	.8729
Hopkins verbal learning	.086	.082	.010	-.001	31	.001	-.276	.084	.010	44	.7263	.1362	.7642	.9681
Digit span forward	-.021	-.156	-.100	.117	31	.227	.118	.143	.143	43	.3077	.2627	.3222	.2891
Digit span backward	-.103	.120	-.182	.072	31	.234	.069	.051	-.017	43	.1645	.8337	.3421	.7188
Spatial span forward	-.325	-.290	-.150	-.340	31	.247	.231	.174	.242	42	.0173*	.0308*	.1868	.0151*
spatial span backward	-.080	-.078	-.086	-.017	30	.139	.141	.098	.224	42	.3789	.3789	.4593	.3271
MMSE						.009	.074	.057	.143	43				
ADAS						-.122	-.129	.020	.115	44				
GDS						-.355*	-.171	-.094	-.065	42				

*p<.05 but non-significant after correction for multiple tests, **p < .05 after Bonferroni correction

4. Discussion

The goal of the present study was to bridge the gap between measures of cognition with physiological markers of healthy ageing comprising eye-tracking and resting state EEG. Overall performance on the cognitive tests was similar across younger and older adults with the following exceptions. In line with previous research (Craik, & Byrd, 1982; Hasher & Zacks, 1988), slight cognitive deficits were observed as younger adults were better at the working memory and inhibitory control tasks compared to older adults. Vocabulary knowledge was superior in older adults, this was anticipated as vocabulary develops with age (Verhaeghen, 2003) and indicates intact ability in the older sample, as did healthy scores on depression and dementia measures. As expected older adults exhibited reduced peak alpha frequency compared to younger adults (e.g., Klimesch, 1999), and older adults also had increased beta activity (Dustman, Shearer, & Emmerson, 1999), but we did not replicate existing research showing age differences in alpha power (e.g., Klimesch, 1999). Older adults showed deficits in accuracy and response times for eye-tracking measures, but these were similar for prosaccades and for eye-tracking tasks linked to inhibition; namely, antisaccades and go/nogo eye-tracking performance. Thus, the age differences in eye-tracking data did not distinguish between prepotent and inhibitory response performance. This could be due to the intact alpha power found in older adults, which has been linked to saccadic performance as summarised in the introduction (e.g., Hamm, Sabatinelli, & Clementz, 2012). Two interaction effects were found in the data. Total (non-localised) beta power was positively related to prosaccade response times such that greater power was related to slower/poorer performance and this relation was present for young but not older adults. Central delta power was negatively related to trail making test part B (inhibition/task switching) such that greater power resulted in faster/better performance, this relation was present for older adults, but not young adults.

Differences in EEG activation across the younger and older age groups may suggest normal changes in brain activity as a result of healthy ageing. Increased beta activity in the older adult group compared to the younger group is consistent with findings that suggest that beta increases with age (before declining at age 60, Dustman et al., 1993). Additionally, decreased alpha peak frequency has been previously reported with increasing age (Scally et al. 2018), as well as alpha power suppression in conjunction with increased beta power (Barry & De Blasio, 2017). Taken together, these changes in resting state EEG add to evidence that suggests increased beta and reduced alpha peak frequency in older adults are biomarkers of healthy ageing as none of our older participants showed impairments in the dementia screening tests. To extend these findings we wanted to examine the relationship between resting state EEG and working memory as previous research suggests that increased theta activity at frontal and parietal sites may be indicative of healthy ageing (Finnigan & Robertson, 2011). In the current study, theta activity was not significantly associated with performance on any of the cognitive

tests which is in contrast to Finnigan and Robertson's (2011) findings, although we used different measures of verbal working memory and attention. Finnigan and Robertson found that increases in theta were related to increased accuracy on auditory verbal learning tests and the sustained attention to respond task, although these associations were rather weak. In our study we found that higher peak alpha frequency corresponded to increased working memory span (before correcting for multiple tests) which is aligned with Clark et al. (2004), whereas Finnigan and Robertson found no relations between cognitive performance and peak alpha frequency.

Vlahou et al. (2014) found that for older adults, there was a positive association between delta power and performance on the trail making task which we replicated in the current study as well as their interaction such that the relation was less evident in young adults. They also found the same interaction with theta activity and our results also numerically replicated that finding. Our data also showed a trend for the same interaction with spatial span for both delta and theta power bands. The pattern was most evident in our data for the trail making task part B, which requires participants to switch between a letter-based trail and a digit-based trail on each increment of the task. Neuroimaging research has shown distinct regions of activation for processing letters compared to digits (e.g., Libertus, Brannon, & Pelphrey, 2009), with theory developing around a number form area in the inferior temporal gyrus (Yeo, Wilkey, & Price, 2017), and visual word form area in the fusiform gyrus (McCandliss, Cohen, & Dehaene, 2003). It has been hypothesised that slow-wave oscillatory activity facilitates communication across distributed neuronal networks (Ahnaou et al. 2014). It may therefore be the case that older adults with naturally higher power in slow-wave delta activity are more resilient to age related decline in this cross-cortical task.

Although there was no age difference in total alpha power the data did show greater asymmetry in parietal alpha power for young adults than for older adults during the eyes closed resting state. This is congruent with a general reduction in asymmetrical neuroactivity with age as hypothesised by Cabeza (2002) although spatial resolution of EEG data means the current results should be interpreted with caution. Figure 5 also shows this age difference in asymmetry is driven by lower parietal power in the right hemisphere of older adults which is congruent with age differences in resting state alpha activity reported by Barry and De Blasio (2017) and potentially is linked to literature showing a right hemisphere vulnerability to ageing (see Hatta et al., 2015, for a review). Hatta et al. also argued that right hemisphere vulnerability to ageing is evidenced by older adults' relatively intact ability on verbal tasks but greater age deficits on visuospatial tasks. Our data showed this pattern of age deficits in cognitive performance and additionally our parietal alpha asymmetry measure showed a significant relation to forwards spatial span scores in a regression model which disappeared after accounting for age. A variety of literature links parietal activity to visuospatial processing including working

memory (e.g., Zago, & Tzourio-Mazoyer, 2002; Klingberg, Forssberg, & Westerberg, 2002) and pointing (Hagler, Riecke, & Sereno, 2007), which is used in the spatial span task.

The eye-tracking data did not replicate existing research which typically shows larger age deficits for inhibitory demanding antisaccades compared to prosaccades (Abel & Douglas, 2007; Peltsch et al., 2011), although we did find a general age deficit in saccadic performance and this was numerically larger for antisaccade accuracy than for prosaccade accuracy as shown in Figure 2. Our saccade error rates were relatively high, even for prosaccades, but these still match around 20% of studies as reviewed by Smyrnis 2008). This is potentially due to our assessment of every saccade start and end point to determine accuracy as opposed to defining accuracy from fixations falling in areas of interest (c.f., Unsworth, Schrock, & Engle, 2004). For the go/nogo eye-tracking task, accuracy was higher than for the prosaccade and antisaccade tasks whilst response times were lower. This suggests a different response bias was driving both tasks in terms of speed-accuracy trade-offs, but such effects were comparable for both age groups. Prosaccade response time was related to total beta power and this effect was largely driven by young adults such that increased beta power led to slower/poorer performance, whilst older adults did not show such a relation. The general higher beta power and slower prosaccade performance in older adults was therefore congruent with the low-performing young adults. Our results are congruent with studies linking beta suppression to increased attentional engagement to visual tasks (Bauer et al., 2006; Hoogenboom et al., 2006; Siegel et al., 2008; Scheeringa et al., 2011) but not studies linking beta activity to alertness and vigilance (Gola at al., 2012; 2013).

Additionally, our relation between beta power and saccadic performance was only present for prosaccade RTs. As these were the fastest saccade responses of all measures taken, this suggests that resting beta power is particularly related to automatic prepotent responses. Of all the eye-tracking measures used, prosaccades are minimally susceptible to accuracy errors and it is likely that prosaccade RTs represent minimal speed/accuracy trade-offs. Salthouse (2000) has shown that age deficits in speed are widespread and can explain a variety of age deficits in cognition. He has argued for increased psychophysiological and neurobiological research to establish the underlying mechanisms behind these observations and our data suggest that beta activity may correspond to fundamental changes in response speed that differ across age.

The current data did not replicate existing research showing reduced reactivity in older adults compared to young adults, that is, a reduced change in activity from eyes closed to eyes open. Barry and De Blasio (2017) found that delta, theta, alpha and beta changes between eyes closed and eyes open EEG were smaller for older adults than for young adults. Reduced reactivity in alpha power was also found in older adults by Duffy et al. (1984) and by Könönen, and Partanen (1993). It is unclear

why these results were not replicated although this could be tied to the fact that alpha power, in general, was similar for both age groups in our sample. Reduced alpha reactivity has been specifically linked to dementia in comparison to healthy older controls (van der Hiele et al., 2008). This new discrepancy may warrant future investigation if reactivity can potentially dissociate healthy from unhealthy ageing. Indeed, it has been argued that task-relevant EEG activity may be insightful for developing links between cognition and ageing (Cummins, & Finnigan, 2007). By measuring EEG in experimental research, age differences in reactivity could be explored in non-correlational paradigms and across a wider variety of tasks than the existing research contrasting activity between eyes open and eyes closed. For example, in their dementia research, van der Hiele et al. (2008) found reactivity in a memory task was smaller for patients than for controls.

A limitation of the present study is that the sample of older adults used is a self-selecting sample. Therefore, their performance on the cognitive tasks may not be representative of the wider population, although the overall pattern of behavioural results was consistent with previous research, some anticipated age deficits were not present and we may have had a particularly able older sample. For example, we did not find age deficits in the digit span tasks as indicated in a meta-analysis (Bopp, & Verhaeghen, 2005), although our result was not particularly unusual and a small proportion of studies in the meta analyses actually showed the opposite result with an older adult advantage. To help address such issues, future research could extend the present findings by employing a similar Eyetracking paradigm and comparing young adults with healthy older adults and patients with mild cognitive impairment (c.f. Crawford et al. 2005). This would aid our understanding of physiological markers for cognitive decline and potentially dissociate theories of healthy and unhealthy ageing. For example, Kavcic, Zalar, and Giordani (2016) found links between slower decision making and delta and theta resting-state EEG in patients reporting memory problems. Furthermore, we use untransformed spectral data. Whilst logarithmic transformations are not expected to effect group comparisons, they have been shown to result in more normally distributed spectral data and thus may have impacted correlation analysis.

The present data indicate that resting state EEG is not only related to cognitive performance but that EEG changes across the lifespan correspond to age-related behavioural changes. This supports ongoing causal research seeking to alleviate age-related cognitive decline. For example, pharmaceutical manipulation of neuroactivity is of key interest to those seeking to alleviate dementia symptoms (e.g., Ahnaou et al. 2014) and targeted magnetic stimulation of the cortex (currently used in the treatment of depression: e.g., McClintock et al. 2018) also has implications for therapeutic treatment of dementia (Sabbagh et al. 2019). Assessing such interventions by EEG and behavioural measures would elucidate if the interventions are being operationalised neurophysiologically in the same way as a healthy/high-performing older adult. Furthermore, much research has focused on EEG

as a biomarker for cognitive decline and dementia (Gaubert et al. 2019) and here we have supported this literature by establishing age-related EEG changes linked to speed, executive function and working memory deficits which are all associated to dementia (e.g., Stopford et al., 2012).

4.1 Conclusion

Our data replicated many established effects in ageing, EEG and eye-tracking. Much is understood about how age and EEG individually relate to task performance and our data have extended this research by providing evidence that age differences in neuroactivity correspond to age differences in task performance. Our current data indicate that areas of interest with respect to future ageing and neuroactivity research would be (i) paradigms linking delta activity to the trail making task B or other measures of inhibition and task switching and (ii) studies linking beta activity to prosaccade task performance or other simple response based perceptual paradigms.

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Appendix

Table A1.

Results for Four Factor ANOVA on EEG power: Age Group (Young, Older) x Condition (Eyes Open, Eyes Closed) x Site (Frontal, Parietal, Temporal, Central, Occipital) x Hemisphere (Left, Right) Reported separately for Power in the Delta and Theta Range

Effect		Significance	Effect Size η_p^2
Delta power			
	Age Group	0.334	0.013
	Condition	0.564	0.005
	Site	0.000	0.464
	Hemisphere	0.297	0.015
	Condition X Age Group	0.996	0.000
	Site X Age Group	0.063	0.033
	Hemisphere X Age Group	0.247	0.018
	Condition X Site	0.014	0.054
	Condition X Site X Age Group	0.292	0.017
	Condition X Hemisphere	0.057	0.049
	Condition X Hemisphere X Age Group	0.274	0.016
	Site X Hemisphere	0.043	0.037
	Site X Hemisphere X Age Group	0.836	0.004
	Condition X Site X Hemisphere	0.320	0.016
	Condition X Site X Hemisphere X Age Group	0.215	0.021
Theta power			
	Age Group	0.421	0.009
	Condition	0.000	0.237
	Site	0.000	0.343
	Hemisphere	0.655	0.003
	Condition X Age Group	0.502	0.006
	Site X Age Group	0.244	0.019
	Hemisphere X Age Group	0.297	0.015
	Condition X Site	0.000	0.195
	Condition X Site X Age Group	0.514	0.008
	Condition X Hemisphere	0.118	0.033
	Condition X Hemisphere X Age Group	0.365	0.011
	Site X Hemisphere	0.000	0.066
	Site X Hemisphere X Age Group	0.542	0.009
	Condition X Site X Hemisphere	0.001	0.087
	Condition X Site X Hemiphere X Age Group	0.251	0.019

Table A2.

Means (and SD) for Delta and Theta Power Split across Age Group (Young, Older) x Condition (Eyes Open, Eyes Closed) x Site (Frontal, Parietal, Temporal, Central, Occipital) x Hemisphere (Left, Right) Reported separately for Power in the Delta and Theta Range

Age	Condition	Site	Hemisphere	Delta	Theta
Young	Eyes open	Frontal	Right	2.17(1.2)	1.39(0.5)
			Left	2.38(0.9)	1.539(0.6)
		Parietal	Right	1.25(0.7)	1.18(0.9)
			Left	1.30(1.0)	1.15(0.7)
		Central	Left	0.77(0.4)	0.70(0.3)
			Right	0.67(0.3)	0.66(0.3)
		Occipital	Right	1.69(1.2)	1.61(1.7)
			Left	1.66(1.1)	1.67(1.7)
		Temporal	Right	1.51(0.9)	1.42(0.7)
			Left	1.89(1.2)	1.33(0.6)
	Eyes closed	Frontal	Right	1.82(0.7)	1.48(0.6)
			Left	2.15(0.9)	1.70(0.8)
		Parietal	Right	1.54(1.0)	2.01(1.9)
			Left	1.35(0.9)	1.55(1.2)
		Central	Right	0.67(0.3)	0.80(0.4)
			Left	0.75(0.4)	0.87(0.5)
		Occipital	Right	1.87(1.3)	2.15(1.7)
			Left	1.86(1.3)	2.33(1.9)
		Temporal	Right	1.41(0.8)	1.47(0.7)
			Left	1.59(0.9)	1.48(0.8)
Older	Eyes open	Frontal	Right	2.19(1.4)	1.35(0.7)
			Left	2.46(1.6)	1.39(0.6)
		Parietal	Right	1.03(0.5)	0.96(0.4)
			Left	1.08(1.0)	0.91(0.3)
		Central	Left	0.82(0.4)	0.67(0.2)
			Right	0.94(0.6)	0.74(0.3)
		Occipital	Right	1.34(0.6)	1.12(0.4)
			Left	1.48(1.0)	1.29(0.6)
		Temporal	right	1.34(0.6)	1.28(0.7)
			Left	1.42(0.6)	1.22(0.6)
	Eyes closed	Frontal	Right	2.00(1.0)	1.60(0.7)
			Left	2.07(1.1)	1.56(0.7)
		Parietal	Right	1.17(0.6)	1.72(1.3)
			Left	0.98(0.4)	1.42(0.8)

Central	Left	0.74(0.2)	0.84(0..3)
	Right	0.86(0.5)	0.88(0.3)
Occipital	Right	1.59(1.9)	2.01(1.5)
	Left	1.31(0.6)	2.05(1.3)
Temporal	Left	1.47(0.8)	1.50(0.7)
	Right	1.44(0.7)	1.50(0.8)