Alterations in rhythmic and non-rhythmic resting-state EEG activity and their link to cognition in older age

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ABSTRACT

While many structural and biochemical changes in the brain have previously been associated with older age, findings concerning functional properties of neuronal networks, as reflected in their electrophysiological signatures, remain rather controversial. These discrepancies might arise due to several reasons, including diverse factors determining general spectral slowing in the alpha frequency range as well as amplitude mixing between the rhythmic and non-rhythmic parameters. We used a large dataset ($N = 1703$, mean age 70) to comprehensively investigate age-related alterations in multiple EEG biomarkers taking into account rhythmic and non-rhythmic activity and their individual contributions to cognitive performance. While we found strong evidence for an individual alpha peak frequency (IAF) decline in older age, we did not observe a significant relationship between theta power and age while controlling for IAF. Not only did IAF decline with age, but it was also positively associated with interference resolution in a working memory task primarily in the right and left temporal lobes suggesting its functional role in information sampling. Critically, we did not detect a significant relationship between alpha power and age when controlling for the 1/f spectral slope, while the latter one showed age-related alterations. These findings thus suggest that the entanglement of IAF slowing and power in the theta frequency range, as well as 1/f slope and alpha power measures, might explain inconsistencies reported previously in the literature. Finally, despite the absence of age-related alterations, alpha power was negatively associated with the speed of processing in the right frontal lobe while 1/f slope showed no consistent relationship to cognitive performance. Our results thus demonstrate that multiple electrophysiological features, as well as their interplay, should be considered for the comprehensive assessment of association between age, neuronal activity, and cognitive performance.

1. Introduction

Older age is often associated with changes in the neuronal brain signals and a consecutive cognitive decline (Gaál et al., 2010; Meunier et al., 2014; Rossini et al., 2007), however, a number of contradictory findings (presented below) suggest that the association between these parameters remains rather unclear. Synchronous firing of pyramidal neural cells involved in the generation of rhythmic oscillatory

activity in different frequency ranges can be measured with scalp EEG (Biasiucci et al., 2019; Buzsáki and Draguhn, 2004; Niedermeyer and Lopes da Silva, 2005) and is typically defined by power, peak frequency, and phase. While all of these parameters have been previously linked to various cognitive functions (Buzsáki, 2006; Grandy et al., 2013; Klimesch, 2012, 1999), alterations in power and peak frequency of different oscillatory bands have been also extensively studied in aging (Ishii et al., 2017; Knyazeva et al., 2018; Knyazev et al., 2015).

Previous work has shown that theta and alpha oscillations (approx. 4 - 7 Hz and 8 - 12 Hz, respectively) play an important role for cognitive functions (Buzsáki and Draguhn, 2004; Palva and Palva, 2007; Puma et al., 2018). Their involvement in higher cognitive processes has been explained through the top-down control over information processing: An interplay between the oscillatory activity defined by power in alpha and theta frequency bands enables suppression of task irrelevant information that helps direct attention towards task relevant stimuli (Jensen et al., 2002; Klimesch, 2012; Palva and Palva, 2007). Power and peak frequency of alpha oscillations have been linked to structural and biochemical alterations in the brain, which is most prominent in older age (Babiloni et al., 2006; Kumral et al., 2021; Stomrud et al., 2010). While most studies consistently show age-related slowing of individual alpha peak frequency (IAF; Ishii et al., 2017; Knyazeva et al., 2018; Mizukami and Katada, 2018), previous findings are inconsistent regarding changes in oscillatory power of theta and alpha oscillations: While alpha power has been suggested to either decline with age (Lodder and van Putten, 2011; Rossini et al., 2007) or show no age-related alterations (Caplan et al., 2015; Sahoo et al., 2020), theta power has been shown both to decline (Vlahou et al., 2015) and increase (Babiloni et al., 2006; Ishii et al., 2017; Klass and Brenner, 1995) with age.

On the one hand, these inconsistencies might be due to power estimation in canonical, rigidly pre-defined frequency bands: If a possible center frequency shift is not accounted for (i.e., in a case of spectral slowing represented by a decrease in IAF), power estimation of two signals in different but neighboring frequency ranges might be confounded. For instance, it has been suggested that slowing of the IAF might interfere with the conventional theta frequency range and thus result in a spurious power increase due to the presence of a low-frequency alpha peak (Finnigan and Robertson, 2011). This could potentially explain inconsistencies in findings associated with theta power changes with age.

Slow-wave power estimation might be confounded not only by a center frequency shift but also due to the amplitude mixing between the oscillatory (i.e., rhythmic) and non-oscillatory (i.e., non-rhythmic) activities (Donoghue et al., 2020; Voytek et al., 2015). Non-rhythmic activity results from asynchronous spiking and postsynaptic potentials of neural populations (Donoghue et al., 2020; Ouyang et al., 2020) and it can be estimated with the 1/f slope of the power spectral density (PSD). The non-rhythmic component of the PSD reflects the ratio between excitatory and inhibitory inputs, as determined by glutamatergic and GABAergic connections, respectively (Donoghue et al., 2020; Gao et al., 2017; Wang, 2020). An increase in excitatory connections was associated with a flatter PSD slope, as compared to an increased number of inhibitory connections, which resulted in a steeper PSD slope. This relationship has been further supported by pharmacological intervention studies of altered states of consciousness (Colombo et al., 2019; Lendner et al., 2020). Age-related changes in 1/f slope have been addressed in a few previous studies showing that the slope decreases as we age, suggesting an increase in excitability and neural noise (Dave et al., 2018; Voytek et al., 2015). However, this relationship has been shown in a wide age range consisting of groups of individuals often distanced by 50 years and it has not been consistently investigated in a narrow age range of, for example, older individuals. Therefore, age-related alterations within a more homogeneous sample of older individuals need further investigation.

Importantly, when controlling for 1/f decay of PSD (decomposing oscillatory and non-oscillatory estimates of PSD), no age-related alterations were shown in slow wave (<12 Hz) power (Caplan et al., 2015).

Furthermore, only few studies have investigated the association between non-oscillatory activity estimated with 1/f slope and cognition: It has been linked to cognitive speed (Ouyang et al., 2020), lexical prediction (Dave et al., 2018), and visual working memory (Voytek et al., 2015).

Given these findings, in the current study, we aimed to disentangle the complex relationship between oscillatory and non-oscillatory resting-state EEG (rsEEG) parameters, age, and cognition. We had the unique opportunity to address this question in a big sample consisting of over 1700 older participants which allowed us to estimate individual contributions of all of the aforementioned measures within a single statistical model including a larger number of predictors. We hypothesized that no age-related alterations in theta and alpha power would be observed when carefully adjusting for methodological confounds, such as spectral slowing and amplitude mixing between the rhythmic and non-rhythmic PSD components. Moreover, based on previous literature, we have also hypothesized a decrease of IAF and 1/f slope with increasing age and that both of these parameters would positively correlate to cognitive performance. We aimed to extend previous work and contribute by investigating this relationship in a group of older individuals with a continuous age span between 60 and 80 years of age.

2. Materials and methods

2.1. Participants

The data used in the present study is a part of the population-based LIFE-Adult dataset (Leipzig Research Center for Civilization Diseases, Leipzig University; Loeffler et al., 2015). Participants were randomly selected from the residence registration office and all participants that agreed to take part in the study provided written informed consent, and received monetary compensation. The study was approved by the ethics board of the Medical Faculty of the University of Leipzig.

EEG data was available from 3390 participants. Our inclusion criteria for the study consisted of completion of cognitive tests (described in Section 2.4.1.), right-handedness, no history of brain hemorrhage, concussion, skull fracture, brain surgery or brain tumor, and no use of medication with an effect on the central nervous system. We also controlled for the vigilance of a resting state recording (described in Section 2.2.) to assure homogeneous levels of arousal and sleepiness throughout the whole sample. After administering these criteria, our final sample consisted of 1703 subjects' (M_{age}=70, SD=4.7, 880 females) datasets.

2.2. Resting-state EEG recordings and pre-processing

A 20 min eyes-closed rsEEG data was recorded from 31-channel Ag/AgCl scalp electrodes (Brain Products GmbH, Gilching, Germany) in an electrically shielded and soundproof EEG booth. The electrodes were mounted in an elastic cap (easyCAP, Herrsching, Germany) according to the international standard 10–20 extended localization system. The signal was amplified with a QuickAmp amplifier (Brain Products GmbH, Gilching, Germany). Additionally, two electrodes recorded vertical (vEOG) and horizontal (hEOG) eye movements above and beneath the right eye. One bipolar electrode attached to the right and left forearm recorded electrocardiogram (ECG). The electrodes were referenced to the common average reference with AFz being a ground electrode. The electrodes' impedances were kept below 10kΩ, the sampling rate was 1000 Hz, and the data was lowpass filtered at 280 Hz. A more detailed description can be found in a paper by Jawinski and colleagues (Jawinski et al., 2017).

EEG data was pre-processed using the MATLAB-based (MathWorks, Inc, Natick, Massachusetts, USA) EEGLAB toolbox (version 14.1.1b) and custom written scripts. First, the data was band-pass filtered between 1 and 45 Hz (4th order Butterworth filter applied back and forth) with a notch filter at 50 Hz to remove any remaining power line artifacts. The data was then downsampled to 500 Hz. We excluded vEOG, hEOG, and ECG channels from the dataset and visually inspected the PSDs of the

multi-channel data of all subjects to determine whether data was contaminated by noise and to identify broken channels. A semiautomatic pipeline was used to mark and remove the segments contaminated by artifacts that corresponded to muscle activity or non-biological noise. For this purpose, we set different amplitude threshold levels for the noise detection at slow-frequency (1–15 Hz) and high frequency (15–45 Hz) ranges. For the slow-frequency range the individual noise threshold was defined as three SD above the mean amplitude of the filtered signal. We set a constant amplitude threshold of 40μV for the high-frequency range. Recordings for which the total bad segment length exceeded 60 s were inspected visually to confirm that the marked segments were indeed contaminated by noise. Independent component analysis (ICA, Infomax (Bell and Sejnowski, 1995)) was applied and artefacts related to eye blinks, eye movements, heartbeat, and muscle activity were removed.

Resting-state EEG recordings are marked by different brain arousal stages that over time shift from alertness to drowsiness and even sleep. Due to the heterogeneity in the arousal and vigilance of the participants, we only used data segments of recordings that had been classified as 'wakeful rest' based on the Vigilance Algorithm Leipzig (VIGALL 2.0, Huang et al., 2015; Jawinski et al., 2017). VIGALL is an automatic algorithm implemented in the Brain Vision Analzyer 2 (Brain Products GmbH, Gilching, Germany), that classifies each one second epoch of the rsEEG recording into seven categories corresponding to estimated brain arousal levels ranging from high alertness to sleep onset. The level of arousal is determined by the combination of power in different frequency bands, the EOG channel activity, and sleep spindles, as well as topographical distribution of these parameters. Based on VIGALL classification, stage A defines wakeful rest that is determined based on the presence of the current density activity distribution in the alpha frequency range (for more detail see the manual at https://research.uni-leipzig.de/vigall/). Stages of VIGALL had been successfully linked to the self-rated likelihood of having fallen asleep (Jawinski et al., 2017) and autonomic nervous system activity (Huang et al., 2018). In the current study we included participants that had at least 5 min of rsEEG data that was classified as stage A. Based on this criterion, 967 participants did not have sufficiently long vigilant rsEEG recordings. For comparability, we controlled the length of the recording across participants and analyzed the first 5 min of every recording.

2.3. EEG data analysis

2.3.1. Rhythmic and non-rhythmic components of the power spectral density

The PSD of each channel's data was calculated from the cleaned data using 4 s Hamming windows overlapping by 50% using Welch's method. We used the Python (version 3.6.7) implementation of the FOOOF algorithm (Donoghue et al., 2020) on the PSDs to estimate the slope of the $1/f$ decay for each channel separately: Here, broad-band PSD between 2 and 40 Hz was modeled as $P(f) \sim 1/f^{\gamma}$ where γ is the spectral slope (see Fig. 1). We did not use the knee parameter. Because the algorithm models Gaussian peaks above the $1/f$ decay of the PSD and fits two Gaussian peaks in case the peak of the original data is non-Gaussian, we did not use features of periodic components extracted by the FOOOF algorithm. After subtracting the $1/f$ part of the spectrum from the original PSD, we performed a peak search between 7 and 13 Hz to localize the alpha peak in each channel. A peak was localized if the inclination (defined as a datapoint that is larger than its neighboring data samples) of the PSD in this frequency range exceeded 0.05 μV^2/Hz. We always took the peak with the highest prominence in case several peaks were found in the frequency range of interest. To define the width of the peak, a horizontal line was extended to the left and right at the point at 10% of the prominence of the peak. In case the width was higher than 6 Hz, we set it to 3 Hz anchored around the maxima of the peak. In case the peak could not be detected, we did not estimate power in that particular channel. We then calculated alpha power as the area under the residual PSD within the frequency range between the start and end of the detected alpha peak. This measure was calculated for each channel of every participant and was then used for further analyses with cognitive scores (described in Section 2.4.). Out of the whole sample included in the current study ($N = 1703$), we could not detect an alpha peak for 1 participant in any of the channels and 13 participants had no peak in more than 15 channels.

We also performed a peak search between 4 and 7 Hz to estimate theta peak parameters using the same criteria that were applied for the alpha peak detection. Only ~3% of participants had an oscillatory peak in this range. We compared this result with the results obtained from the FOOOF algorithm. Based on the FOOOF peak parametrization, out of 1703 participants included in our study, 781 had no theta peak detected in any of the channels, and 1015 participants had no detectable theta peak in any of the 11 frontal and fronto-central channels. Therefore, we estimated theta power in a frequency range between the starting point of the alpha peak and 3 Hz before it. Power in this range was estimated using the original PSD (containing the non-rhythmic component) since the subtraction of $1/f$ might cause negative values in the residual of the PSD. We inspected data for outliers based on the interquartile range (IQR (49))). We defined an outlier as a data value that exceeded an interval of $q_3 + 3 * IQR$, where q_3 is the third quartile for alpha and theta power and we additionally used an interval of $q_1 - 3 * IQR$ for the negatively skewed values of $1/f$ slope values, where q_1 is the first quartile.

2.3.2. EEG source reconstruction

For every significant relationship at a sensor level, we performed a source localization. We built individual head models for those participants that had an MRI scan (n~700) and used a standard head model for the rest of the subjects. For the individual head models, we used the T1-weighted MPRAGE images that were acquired with a 3 Tesla Verio scanner (Siemens, Erlangen, Germany) and were segmented using the Freesurfer v.5.3.0 software (Fischl, 2012). A 3-shell boundary element model was constructed with Brainstorm (Tadel et al., 2011), which was used to compute the leadfield matrix with OpenMEEG (Gramfort et al., 2010). The standard head model was based on the ICBM152 nonlinear average head anatomy (version 2009) included within Brainstorm. Electrode positions were registered to the scalp surface of the standard head according to the 10–20 electrode placement. For individual head models, electrode positions were warped from the standard to the individual anatomy using SPM (Frackowiak et al., 1997). In all cases the source space consisted of ca. 2000 voxels located on the cortical mantle. We constrained the orientation of the dipolar sources to be perpendicular to the cortical surface. Source reconstruction was performed using exact low-resolution brain electromagnetic tomography (Pascual-Marqui, 2009) with a regularization parameter of 0.05 implemented in the M/EEG Toolbox of Hamburg (METH, https://www.uke.de/english/departments-institutes/institutes/neurophysiology-and-pathophysiology/research/research-groups/index.html). Due to the small number of EEG channels ($N = 31$), we grouped the cortical vertices into 10 major regions (ROIs) that were aggregated based on the 68 regions of the Desikan-Killiany atlas (Desikan et al., 2006): We used a geometric mean for theta and alpha power, mode for the IAF, and median for the $1/f$ slope. The rest of the analysis was done in the same way as described in Section 2.3.1.

2.4. Cognition battery

2.4.1. Description of cognitive tests

We used data from four cognitive tests: the Trail Making Test (TMT; (Reitan, 1956)), Stroop test (Scarpina and Tagini, 2017), Wechsler's Memory Scale (Wechsler, 2009), and Vocabulary Knowledge Test (org. Wortschatztest, WST; (Schmidt and Metzler, 1992)). That were used as a proxy for processing speed, mental flexibility, interference resolution, memory, and crystalized intelligence. We inverted the reaction time scores ($1/s$) for interpretability, where higher scores meant better performance. We visually inspected cognitive scores for possible outliers

and removed data in case of values associated with a typing error. We then z-transformed all scores after outlier removal.

2.4.2. Factor analysis of the cognition battery

Exploratory factor analysis (EFA) was used to extract latent factors underlying cognitive scales (*stats* package R (version 3.4.4)). The number of latent factors was determined by the Scree plots as well as the Empirical Kaiser Criterion (EKC, (Braeken and van Assen, 2017)), according to which only the components with eigenvalues larger than one should be kept. Both, the Scree plots as well as EKC, suggested three latent factors that explained 67% of the variance in the data. These three factors were used for further statistical analyses.

2.5. Statistical analyses

2.5.1. Relationship between resting-state EEG parameters and age

To test the relationship between the PSD components and their link to age, we used a mass-bivariate approach and cluster-based statistics (Maris and Oostenveld, 2007) to correct for multiple comparisons across channels. For every relationship between the rsEEG parameters and age in each channel we used Pearson partial correlations. We partialed out the effects of the three other PSD variables as well as sex (measured as a bivariate choice between 'male' and 'female') and education. Then, clusters were formed in sensor space defined as several neighboring channels with the significance threshold of $p<0.05$. If a cluster was found, the cluster t-value, estimated as a sum of t-values over electrodes that formed the cluster, was compared to a null distribution of clusters generated using the Monte Carlo method with 1000 permutations of the age values. By comparing the t-value of the original cluster with the randomly generated ones, we determined the corresponding cluster p-value ($p_{cluster}$). A cluster was considered significant if $p_{cluster} \leq 0.0125$ (Bonferroni correction).

While investigating the relationship between alpha power and age prior to the subtraction of the 1/f decay (i.e., from the original PSD), we controlled for IAF, sex, and education. However, we did not control for theta power – due to the absence of an oscillatory peak in theta frequency range, theta power would capture properties of 1/f slope that we intended to keep. We also assessed the significance of both clusters that were formed depicting the relationship between alpha power and age, to investigate which regions of the cortex might be most susceptible.

2.5.2. Relationship between resting-state EEG parameters and cognition

To test the relation between the rsEEG parameters and the three cognitive factors, we used multiple linear regression (MLR) with interaction terms for age and rsEEG parameters of interest using the *lm* function implemented in R. We ran separate MLRs for each cognitive factor and 10 ROIs due to high collinearity between brain regions. Multicollinearity might compromise the model as the effects of independent variables on the dependent one could not be reliably estimated in isolation. Therefore, each MLR model consisted of four independent variables of interest (theta power, alpha power, IAF, and 1/f slope), as well as their interactions with age. Age, sex, and education were added as covariates to the models. We corrected for multiple comparisons using false discovery rate at 0.05 (FDR, (Benjamini and Hochberg, 1995)).

3. Results

3.1. Descriptive information

We have analyzed data of 1703 participants ($M_{age}=70$, SD=4.7, 880 females): Demographic information and sample characteristics can be found in *Supplementary material, Table 1,* separately for men and women. Grand average topographies of resting-state EEG features can be seen in Fig. 1.

Measures of theta and alpha power, IAF, and 1/f slope of PSD showed strong correlations among each other with a widespread effect over the
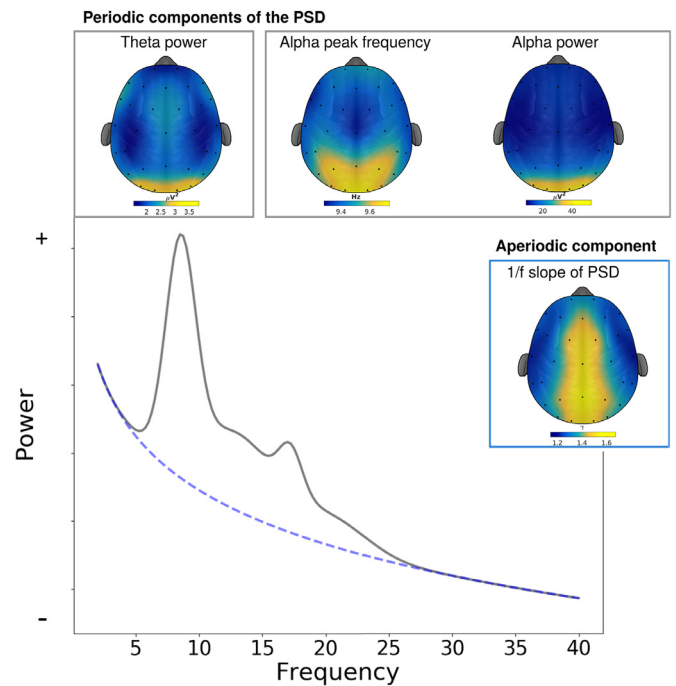

Fig. 1. An exemplary power spectral density of a single EEG channel and grand average topographies of resting-state EEG parameters: Theta and alpha power, individual alpha peak frequency, and 1/f slope of PSD decay (marked with a dashed blue line).

whole cortex (all $p<0.001$, rho values vary between 0.3 and 0.7, p-values were based on Pearson correlation, clusters of electrodes were corrected for multiple comparisons using cluster statistics, *Supplementary material*).

3.2. Resting-state EEG spectral changes associated with age

We used a mass-bivariate approach with cluster-based permutation tests (Maris and Oostenveld, 2007) to assess whether age-related changes occurred in the rsEEG parameters in sensor space. Importantly, alpha power showed age-related reductions before controlling for 1/f slope (Fig. 2, *panel A*) with two clusters at frontal ($p_{cluster}=0.055$) and occipital ($p_{cluster}=0.038$) regions. No significant cluster was observed when estimating alpha power from detrended PSD (i.e., after the subtraction of 1/f decay), suggesting that the aforementioned results might capture age-related alterations in 1/f slope rather than power of alpha oscillations.

A widespread negative relationship between IAF and age ($p_{cluster}<0.001$, Fig. 3, *panel A*) was present at all electrodes. This result was replicated at the source level, where this relationship was significant in all 10 ROIs with the left temporal lobe showing the strongest effect ($p<0.001$, $r=-0.22$). Another cluster of electrodes showing a negative significant relation between 1/f slope and age was detected over the fronto-central electrodes at sensor space ($p_{cluster}=0.012$, Fig. 3, *panel B*). Source reconstruction showed that the significant relationship was detected in the right frontal lobe ($p = 0.001$, $r=-0.08$).

Other rsEEG parameters (i.e., theta power, and alpha power (after controlling for 1/f decay), Fig. 2) showed no significant age-related alterations, either at sensor or at source space. Because sensor space findings matched findings in the source space, source space data were used in the following analyses.
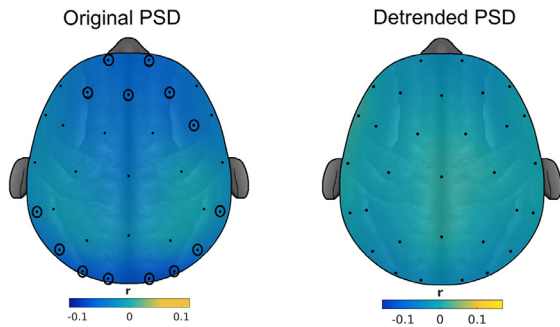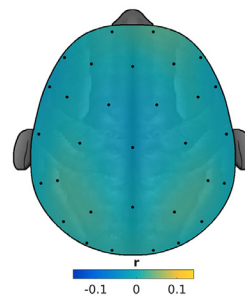
Fig. 2. Age-related alterations in alpha and theta power. Topographies depict correlation coefficients and significant sensors are marked with black circled dots. (A) Alpha power shows a decrease with age primarily in frontal and occipital regions, however, this relationship is absent when controlling for 1/f spectral decay (i.e., measured on detrended PSD). (B) No significant age-related alterations were observed in theta power.
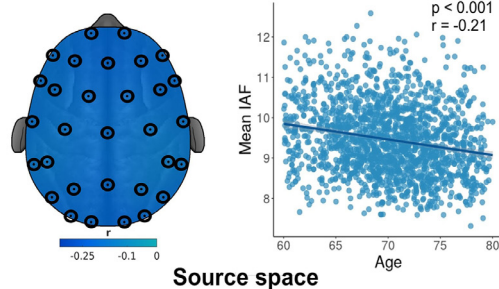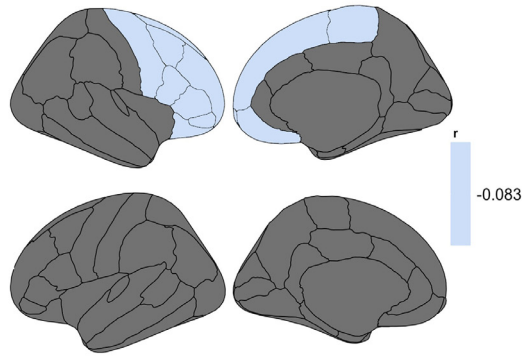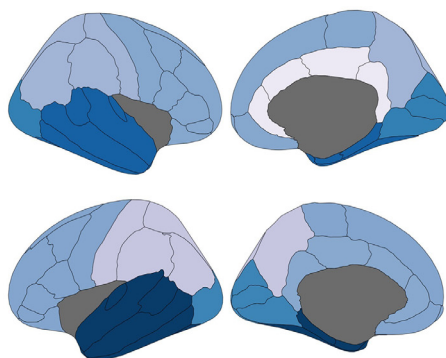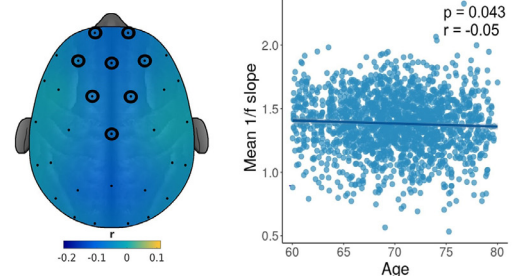

Fig. 3. Age-related alterations in resting-state EEG parameters at sensor and source space. Sensors that formed significant cluster are marked with black circled dots. Scatterplots indicate mean values across significant EEG sensors. (A) Individual alpha peak frequency (IAF) showed a significant negative correlations with age that was prominent over the whole cortical mantle at sensor and source space. (B) 1/f slope of the power spectral density was negatively associated with age at fronto-central channels at sensor space and in the frontal lobe at source space.

3.3. Cognitive performance

3.3.1. Factor analysis

Based on the factor loadings (>0.4), we interpreted three factors as representing *speed of processing, episodic memory*, and *interference resolution*. The first factor, the speed of processing, positively loaded on the reaction times from the congruent and incongruent trials of the Stroop task. The second factor, associated with episodic memory, positively loaded on the Wechsler's Memory Scale, Logical Memory subscales. Finally, the third factor reflecting interference resolution loaded positively on the accuracy of incongruent trials of the Stroop task, and negatively on the inverted reaction times of the same condition. The interpretation of the third factor as interference resolution was based on the increased cognitive demands under the effect of Stroop interference that resulted in slower reaction times but higher accuracy (see Fig. 4, *panel A*). The three identified factors correspond to the main cognitive domains of attention, memory, and executive functions, respectively.

3.4. Relationship between age and cognitive performance

All three factors showed a significant decrease with age (speed of processing: $p<0.001$, rho = -0.12, episodic memory: $p<0.001$, rho=-0.1, interference resolution: $p<0.001$, rho=-0.16; Fig. 4, *panel B*) and were used for the following multiple linear regression (MLR) models.

3.5. Relationship between resting-state EEG parameters and cognitive performance

For simplicity, we report here only the results from regions that were statistically significant (all outputs from the MLR models can be found in *Supplementary material, Tables 1–10*).

Models assessing the relationship between the factor representing interference resolution and rsEEG parameters (*model statistics*: adj. R^2 ranged from 0.03 to 0.04; F(1557) ranged from 5.1 to 7.1, $p<0.001$;
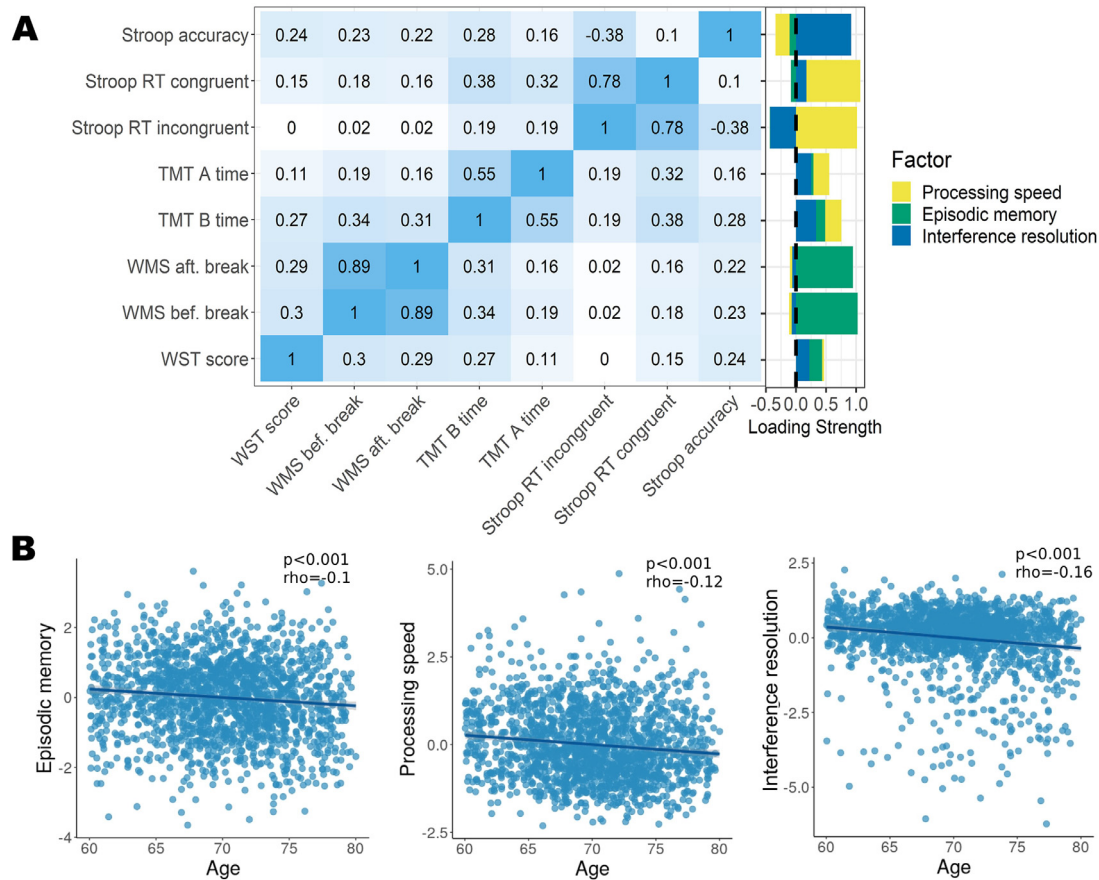
Fig. 4. Three latent factors representing episodic memory, processing speed, and interference resolution derived from the cognition battery. (A) The correlation matrix shows that most of the subscales from the cognition battery were moderately correlated with each other. The loading strength, to the right, represents the contribution of the particular scale to the factor. (B) All of the latent factors showed a decrease with age.

Fig. 5 panels*A-B*) showed a positive association with IAF in six regions: right frontal ($p<0.01$, $\beta=0.07$), right ($p<0.01$, $\beta=0.08$) and left ($p<0.01$, $\beta=0.07$) parietal, right ($p<0.001$, $\beta=0.09$) and left ($p<0.01$, $\beta=0.08$) temporal, and right cingulate cortex ($p<0.01$, $\beta=0.07$). Moreover, age was negatively related ($p<0.001$, βs ranged from -0.14 to -0.15) and education was positively related ($p<0.01$, βs ranged from 0.07 to 0.08) to this factor.

Models for the factor representing the speed of processing revealed a significant negative relationship with alpha power ($p<0.01$, $\beta=-0.08$; Fig. 5 panels *C-D*) in the right frontal region (*model statistics*: adj. R^2:0.017; $F(1557)=3.41$, $p<0.001$). Age was also negatively associated with the factor in this model ($p<0.001$, $\beta=-0.11$). Other independent variables as well as interaction terms between rsEEG parameters and age were not significant.

Models for the factor representing episodic memory were significant (*model statistics*: adj. R^2 ranged from 0.061 to 0.068; $F(1557)$ ranged from 10.35 to 11.36, $p<0.001$), however, they showed no association with the rsEEG measures.

4. Discussion

This study investigated how rhythmic (i.e., theta power, alpha power, IAF) and non-rhythmic (i.e., 1/f slope) rsEEG activity relates to aging and cognition in a large cohort of healthy elderly participants. There were four main findings after we separated periodic and aperiodic components: (i) IAF decreased with age: an effect that was robustly observed across the whole cortex but was strongest in the left temporal lobe; (ii) Age-related alterations were observed in 1/f slope of PSD suggesting flattening of the slope in the right frontal lobe; (iii) No sig-

nificant age-related alterations were seen in slow wave power (alpha and theta frequency), which is in contrast to several previous reports; (iv) Relating individual contributions of rsEEG parameters to cognitive performance, alpha power in the right frontal lobe was negatively associated with processing speed while higher IAF in multiple cortical areas contributed to better interference resolution. In the current manuscript we used a variety of methods and carefully controlled for amplitude mixing of aperiodic and periodic components, slowing of the IAF, as well as vigilance of the EEG recording that has not been consistently controlled for in previous studies.

4.1. Age-related alterations of resting-state EEG parameters

In the current study we show a prominent IAF decrease with age that is consistent with previous reports on age-related spectral slowing (Ishii et al., 2017; Knyazeva et al., 2018; Mizukami and Katada, 2018). Peak frequency slowing might reflect changes on the level of neurotransmission as well as a decrease in axonal conduction velocity (Dustman et al., 1993; Hong and Rebec, 2012). This might, in turn, result in a prolonged time delay within an intra-cortical circuitry and, therefore, slower IAF. Although participants of the current study did not suffer from any neurological condition, slowing of the alpha peak might nevertheless be indicative of neuronal processes that underlie early subclinical stages of neurodegenerative conditions whose prevalence increase with age. This finding is juxtaposed with the observation that higher IAF might contribute to better cognition, and specifically, interference resolution (see below).

Alterations in axonal connections between neurons can affect not only IAF, but can also impact compensatory increases of neural firing
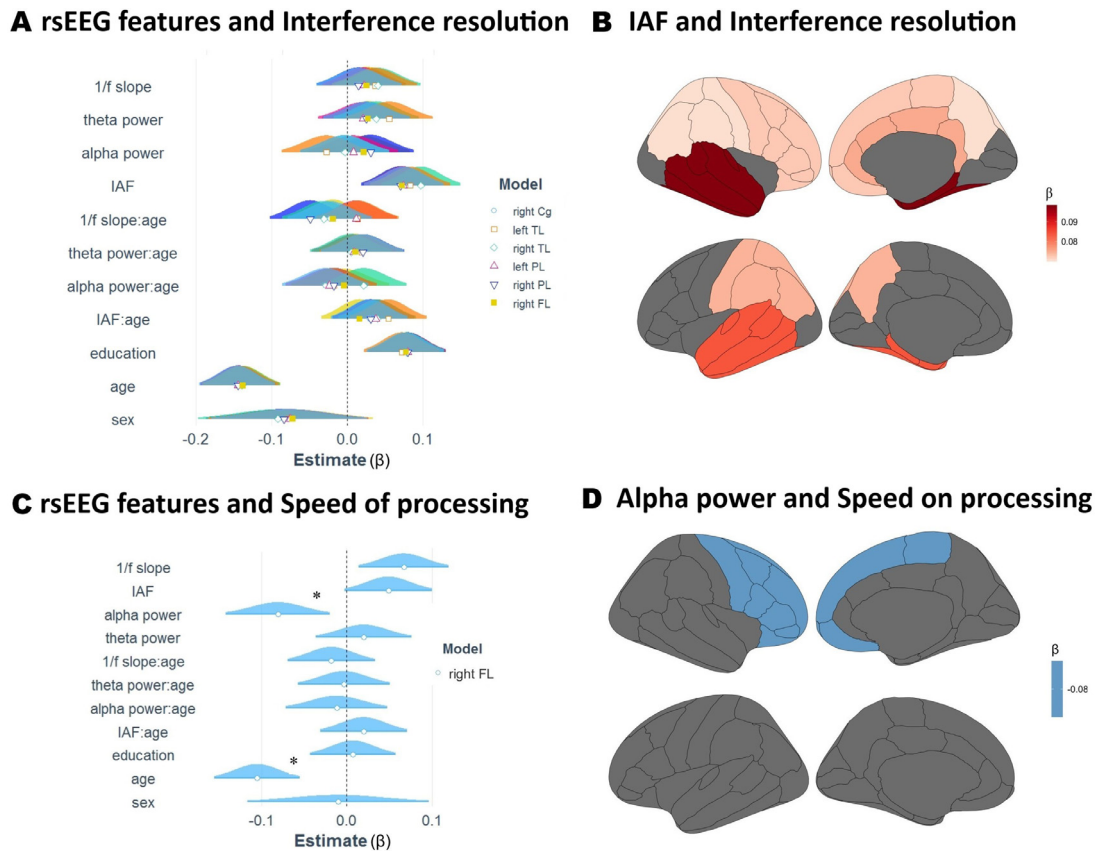
Fig. 5. Relationship between rsEEG parameters and cognition. (A) Based on the linear models, individual alpha peak frequency (IAF) significantly related to the factor representing interference resolution. The figure shows estimates of standardized predictors together with a distribution of their confidence intervals in different regions indicated by colors. Interaction terms are indicated with a colon and significant effects are marked with an asterisk. (B) A positive association between the IAF and interference resolution seen in panel (A) plotted at source space on a cortical mantle. (C) Alpha power was negatively associated with another factor representing speed of processing. This effect was significant in the right frontal lobe but not other regions. (D) The significant relationship in panel (C) plotted at the source space.

rates in higher frequency ranges (Hong and Rebec, 2012) and, consequently, a flatter $1/f$ slope. In line with these findings as well as previous reports of age-related alterations in $1/f$ slope (Dave et al., 2018; Voytek et al., 2015), our results suggest that flattening of the slope might reflect increased cortical excitability and a possible over-recruitment of frontal brain regions in older age (Davis et al., 2008; Nyberg et al., 2010). Importantly, our findings are consistent with previous reports despite the differences in analyzed age-ranges. While previous studies compared younger (20–30 years old) versus older (60–70 years old) participants, we have observed the same effect within a narrow age range between 60 and 80 years.

Despite multiple reports of age-related alterations of power in theta and alpha frequency ranges across the lifespan (Rossini et al., 2007; Vlahou et al., 2015), and within an older age range alone (Lodder and van Putten, 2011), we did not observe significant changes of these parameters. An absence of changes in theta and alpha power might be due to differences in methodology: (i) Individually adjusted frequency ranges of interest based on the center frequency, (ii) the dissociation between rhythmic and non-rhythmic components of PSD, and (iii) the estimation of unique contributions of these parameters. Indeed, we also showed that when the $1/f$ decay of the PSD is not controlled for, a reduction in alpha power could be observed in frontal and occipital regions with a more liberal significance level. This finding suggests that previous reports on age-related alterations in alpha power might result from the mixing of rhythmic and non-rhythmic components of the PSD. Moreover, the absence of age-related alterations in theta power might also suggest that previous reports showing a significant relationship between the two might have been related to IAF slowing. In line with our

findings, Caplan and colleagues (Caplan et al., 2015) did not observe any age-related alterations in theta and alpha band power. While the authors reported a detectable rhythmic activity in the alpha frequency range, it did not alter with age when controlling for non-rhythmic activity (i.e., $1/f$ slope).

4.2. The link between resting-state EEG parameters and cognition

With the second research question, we aimed to explore the link between rsEEG parameters and cognition in old age. We found that reduced alpha power in the right frontal lobe was differentially associated with higher processing speed. When measured at rest, alpha power has been suggested to reflect properties of an attentional filter, which might relate to the ability to inhibit task-irrelevant information when task demands are met (Händel et al., 2011; MacLean et al., 2012). Task-related power reduction in the alpha frequency band has been previously linked to an increase in excitability (Iemi et al., 2019; Klimesch et al., 2007). In line with these previous studies, we suggest that reduced alpha power over the right frontal lobe might represent increased excitability of a network that enables top-down control. Increased excitability in this region might relate to impulsive and fast reactions to stimuli at the expense of accuracy (represented by the processing speed) and might serve as yet another support for functional 'over-recruitment' of frontal brain regions in older age (Davis et al., 2008; Nyberg et al., 2010). Moreover, consistent with our finding, previous reports have also suggested weakened inhibitory activity in older age (Borghini et al., 2018; Dustman et al., 1993). While other parameters used in the current study (e.g. IAF and $1/f$ slope of the PSD) have also been associated with excitability, we

have controlled for their possible effects on the respective cognitive function.

It has been shown that not only alpha power but also instantaneous IAF is related to excitation/inhibition balance and information processing, particularly in the visual domain (Nelli et al., 2017; Samaha and Postle, 2015). While we found a prominent IAF decrease with increasing age, we also observed that IAF was related to interference resolution in a working memory task. Higher IAF over bilateral cingulate cortex, left and right parietal- and temporal-lobes, as well as the right frontal lobe was associated with better interference resolution, specifically with tasks relying on Stroop interference effects. It has been previously suggested that higher IAF relates to a finer temporal sampling of visual information (Samaha and Postle, 2015), also shown in a cross-modal domain (Cecere et al., 2015). The authors have suggested that the number of alpha cycles within which the temporally close stimuli fall facilitates segregation (in contrast to integration) of discrete perception (Samaha and Postle, 2015). Therefore, our findings indicate that while higher IAF corresponds to more oscillatory cycles within the given time window of stimulus presentation, as compared to slower IAF, it might as well facilitate segregation of information resulting from two interfering domains – the color and semantics of the word in the context of a Stroop task. Taking into account a decrease in IAF in older age and its significant relationship with interference resolution, our observation is in line with studies showing reduced capacity to ignore and inhibit interfering information in older age (Li et al., 2001).

5. Conclusion

Taken together, our results provide evidence for the need to consider both rhythmic and non-rhythmic components of the PSD when estimating age-related alterations in resting-state EEG. This is particularly important for power estimation in different frequency bands: We show that when the $1/f$ spectral decay is not controlled for, alterations in alpha power could be observed as a result of the mixing of rhythmic and non-rhythmic components. While we did not observe the previously reported power reduction either in theta or alpha frequency ranges (after detrending the PSD), we confirmed a persistent negative relationship between IAF and age across the entire cortical mantle. Additionally, higher IAF was also related to better interference resolution: This finding suggests that higher IAF may facilitate the segregation of interfering information in older age. Age-related alterations in $1/f$ spectral slope as well as the link between resting-state alpha power and speed of processing possibly suggest increased excitability in the right frontal lobe that may lead to more impulsive responses to stimuli. On the functional level, our findings, therefore, support the notion of functional reorganization of the brain in older age with a possible over-recruitment of frontal brain regions (Davis et al., 2008; Nyberg et al., 2010). It is important to note that we controlled for vigilance of the resting-state EEG recordings using the VIGALL algorithm that has been developed and validated on the same sample of older participants used in the current study.

5.1. Limitations

In the current study we investigated the impact of separating periodic and aperiodic components of the PSD of rsEEG data on commonly reported findings in the aging literature. Extending these findings to task EEG data as well as to other frequency bands would be beneficial to investigate these considerations further. Our dataset included a relatively narrow age range of participants, and further research needs to be performed to investigate these findings in other age groups. Moreover, given our choice of the neuroimaging method, we could not link our findings to other neurobiological changes that are commonly reported in aging literature that would be beneficial in order to understand the full picture of age-related changes in the brain. Finally, we used VIGALL algorithm to classify and control for vigilance of the participants, however, previous studies did not control for it and, therefore, a direct

comparison is difficult to make as the effect of vigilance in those studies remains rather unanswered.

Declaration of Competing Interest

Authors declare no competing financial or non-financial interests in relation to the work.

Data Availability

The authors do not have permission to share data.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2022.119810.

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