Registered Report

Decomposing age effects in EEG alpha power

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A B S T R A C T

Increasing life expectancy is prompting the need to understand how the brain changes during healthy aging. Research utilizing electroencephalography (EEG) has found that the power of alpha oscillations decrease from adulthood on. However, non-oscillatory (aperiodic) components in the data may confound results and thus require re-investigation of these findings. Thus, the present report analyzed a pilot and two additional independent samples (total \( N = 533 \)) of resting-state EEG from healthy young and elderly individuals. A newly developed algorithm was utilized that allows the decomposition of the measured signal into periodic and aperiodic signal components. By using multivariate sequential Bayesian updating of the age effect in each signal component, evidence across the datasets was accumulated. It was hypothesized that previously reported age-related alpha power differences will largely diminish when total power is adjusted for the aperiodic signal component.

First, the age-related decrease in total alpha power was replicated. Concurrently, decreases of the intercept and slope (i.e. exponent) of the aperiodic signal component were observed. Findings on aperiodic-adjusted alpha power indicated that this general shift of the power spectrum leads to an overestimation of the true age effects in conventional analyses of total alpha power. Thus, the importance of separating neural power spectra into periodic and aperiodic signal components is highlighted. However, also after accounting for these confounding factors, the sequential Bayesian updating analysis provided robust evidence that aging is associated with decreased aperiodic-adjusted alpha power. While the relation of the aperiodic component and aperiodic-adjusted alpha power to cognitive decline demands further investigation, the consistent findings on age effects across independent datasets and high test-retest reliabilities support that these newly emerging measures are reliable markers of the aging brain. Hence, previous interpretations of age-related decreases in alpha power are reevaluated, incorporating changes in the aperiodic signal.
1. Introduction

Alpha oscillations are by far the most widely studied phenomenon in human electroencephalography (EEG). Since the beginnings of EEG research in the 1920s, individual differences in alpha oscillations have been linked to variations in behavioral phenotypes and physiology (Bazanova & Vernon, 2014; Klimesch, 1999, 2012). The alpha band is commonly defined as oscillatory activity in the range of frequencies between 8 and 13 Hz (Babiloni et al., 2020; Niedermeyer, 1999). These oscillations are typically observed over parietal and occipital electrode sites (Breslau, Starr, Sicotte, Higa, & Buchsbaum, 1989; Markand, 1990) and show the highest test–retest reliability of all frequency bands (Gasser, Bächer, & Steinberg, 1985). A robust finding is that alpha power decreases during task engagement (e.g., alpha event-related desynchronization). This led to the classical view that alpha amplitude reflects the idle state of cortical areas (Bazanova & Vernon, 2014; Klimesch, 2012). Moreover, modulations of alpha power have been linked to a variety of important concepts ranging from the classical findings on inhibition (Berger, 1929; Jensen and Mazaheri, 2010, 2010, 2010; Klimesch, 1999, 2012) to the blood-oxygen-level-dependent (BOLD) signal (Knight, 2015) and to the blood-oxygen-level-dependent (BOLD) signal (Knight, 2015).

Alpha oscillations are of particular interest in aging research because studies have repeatedly demonstrated that the alpha rhythm’s frequency slows (Klimesch, 1999) and the alpha band power’s amplitude decreases with age (Babiloni et al., 2006; Breslau et al., 1989; Polich, 1997; Roubeick, 1977; Scally, Burke, Bunce, & Delvenne, 2018; Vysata, Kukal, Prochazka, Pazdera, & Valis, 2012). A study investigating alpha power on source rather than on scalp level found age-related decreases particularly in posterior and occipital brain regions (Babiloni et al., 2006). Furthermore, aging studies have often divided the alpha band into lower alpha and upper alpha sub-bands because these sub-bands have been linked to distinct cognitive functions (Babiloni et al., 2020; Klimesch, 1999; Klimesch, Doppelmayr, Russegger, Pachinger, & Schweiger, 1998; Polich, 1997; Scally et al., 2018). Whereas the lower alpha band has been associated with attentional processing (Klimesch et al., 1998), age effects are found particularly in the upper alpha band, and are interpreted as changes of memory operations (Polich, 1997; Scally et al., 2018).

However, these results and interpretations of age-related alpha power changes need to be evaluated critically. Previous findings have demonstrated a slowing of the alpha rhythm with increasing age (Klimesch, 1999), so an age-related shift of the alpha peak frequency could lead to a reduction of alpha power as measured by fixed frequency bands (Scally et al., 2018). This may happen when the individual frequency center nears the lower limit of the fixed frequency band and therefore no longer captures the individual alpha oscillation (Donoghue, Haller, et al., 2020). Thus, the frequency band definition should be based on the individual alpha frequency center to rule out this confound.

More importantly, recent development in EEG signal processing techniques further question earlier findings of decreased alpha power in age (Donoghue, Haller, et al., 2020). It was demonstrated that the band power of the observed frequency consists not only of a periodic, or oscillatory, component but also of an aperiodic, or non-oscillatory, signal. Therefore, band power should be investigated relative to this aperiodic signal (Chiang, Rennie, Robinson, van Albada, & Kerr, 2011; Donoghue et al., 2020a, 2020b; He, 2014; He et al., 2019; Voytek et al., 2015; Wen & Liu, 2016). Recent work by our group further highlighted the importance of taking the aperiodic signal into account in the investigation of age trajectories of alpha power during childhood and adolescence (Tröndle, Popov, Dziemian, & Langer, 2022). The aperiodic signal is characterized by its shape (1/f), as its amplitude decreases with higher frequencies f (see Fig. 1). This is based on the observation that neural power spectra exhibit a static increase in power towards lower frequencies that has been shown to follow an underlying broadband power law with a negative slope (Miller, Sorensen, Ojemann, & Nijs, 2009). In recent years, the aperiodic signal has attracted increasing attention from the research community. This aperiodic signal may not be treated as background noise, as it is related to task performance and arousal states as well as developmental and disease processes (He, 2014). Whereas the offset of the aperiodic signal has been linked to general spiking activity (Voytek & Knight, 2015) and to the blood-oxygen-level-dependent (BOLD) signal.
signal in functional magnetic resonance imaging (Winawer et al., 2013), the slope has been associated with the synchronicity of activity in the underlying neural population (Miller et al., 2009; Usher et al., 1995). A more asynchronous activation pattern has been shown to yield a flatter aperiodic slope. Furthermore, the aperiodic slope may be linked to the excitation–inhibition balance of transmembrane currents (Cao, Peterson, & Voytek, 2017). GABA receptor mediated inhibitory currents show high power at lower frequencies with a fast decay towards higher frequencies, leading to a steeper slope. AMPA receptor mediated excitatory currents show a slower decay of power towards higher frequencies, yielding a flatter slope for the aperiodic signal. Therefore, the higher the ratio of excitatory activity to inhibitory activity, the flatter is the aperiodic slope (Gao et al., 2017).

Thus, decomposing aperiodic activity from periodic appears mandatory in aging research as the aperiodic signal itself seems to change (i.e. flatter slope and decreased intercept) with increasing age (Dave, Brothers, & Swaab, 2018; Donoghue, Haller, et al., 2020; Thuwal, Banerjee, & Roy, 2021; Voytek et al., 2015); hence, it may change the shape of the neural power spectrum even though the oscillatory pattern remains stable. Conventional analyses are prone to conflating periodic and aperiodic signal components and thus may lead to fallacious conclusions (Donoghue, Haller, et al., 2020) and neurophysiological interpretations about age-related changes of alpha oscillations. According to present interpretations, the age related decrease of alpha power results from increased excitability in thalamo-cortical and cortico–cortical interactions (Pfurtscheller & Da Lopes Silva, 1999; Steriade & Llinás, 1988). This is caused by age related loss of cholinergic function of the basal forebrain (e.g., Sarter & Bruno, 1998; Schliebs & Arendt, 2011), which forms major cholinergic input to the thalamus (Sokhadze, Campbell, & Guido, 2019). These interpretations may need to be reconsidered, incorporating the neural noise hypothesis of aging, which states that increases in neural noise (i.e. flatter aperiodic slope) causes age related cognitive decline, by interfering in neural communication (Voytek et al., 2015).

In the present study we addressed this problem by directly comparing previously established age differences in unadjusted alpha power, here referred to as total alpha power, to age effects in the true periodic component of the alpha band, here referred to as aperiodic-adjusted alpha power and the aperiodic signal components, here referred as aperiodic exponent (i.e., slope, the smaller the exponent, the flatter the aperiodic signal) and aperiodic intercept (see Table 1 for an overview of all terms related to the extracted alpha parameters).

One recent magnetoencephalography (MEG) study (Thuwal et al., 2021) investigated age effects in the aperiodic signal and in aperiodic-adjusted power, reporting a decline of aperiodic-adjusted alpha power in the average across all sensors while power specifically in occipital sensors seemed to remain stable. Age effects in total alpha power were not investigated in this sample. So far, only one study compared age effects in the total and aperiodic-adjusted alpha power using a small sample of 16 younger and 14 elderly subjects (Donoghue, Haller, et al., 2020). While significant age-related decreases in aperiodic signal components, total and aperiodic-adjusted alpha power were reported, no statistical test was applied to investigate the particular contrast of age effects on total alpha power with age effects on aperiodic-adjusted alpha power. Both studies (Donoghue, Haller, et al., 2020; Thuwal et al., 2021) did not distinguish between upper and lower alpha bands, as frequently done in aging research (Babiloni et al., 2020; Klimesch, 1999; Klimesch et al., 1998; Polich, 1997; Scally et al., 2018). Altogether, it remains unknown whether the previously found age effects on alpha power are mainly driven by aperiodic, periodic or both signal components. We therefore conducted a rigorous statistical evaluation of age effects in alpha power, taking the aperiodic signal into account, within a reasonably powered sample that allows to draw reliable and robust conclusions about these specific age differences.

A total of 514 subjects were investigated, employing multivariate statistical models to compare age differences in parieto-occipital total alpha power, aperiodic-adjusted alpha power, and aperiodic signal components. The multivariate approach is able to account for the potential correlation between the total and aperiodic-adjusted power measures. Total alpha power was extracted using conventional spectral analysis, which does not adjust for the aperiodic signal. Aperiodic-adjusted alpha power and aperiodic signal components were extracted using the SpecParam (Donoghue, Haller, et al., 2020) algorithm. Fig. 1 illustrates the resulting parametrization of an EEG power spectrum. Alpha power measures were extracted from a canonically defined fixed frequency band (8–13 Hz) and from the individual anchor point (the individual alpha frequency IAF, see Table 1 for more details) to rule out confounds from a slowing IAF on the observed alpha power. Spatial patterns for each parameter were examined by including all electrodes on the full scalp. Source analysis enabled the exploration of the neural generators of the aperiodic and aperiodic-adjusted parameters. The analysis pipeline was first evaluated in a pilot sample of 63 young and 55 older participants. After fixing all analysis parameters using this pilot sample, the same pipeline was applied to the larger dataset of 100 young and 100 elderly subjects. Finally, results were validated using a third, openly available dataset derived from 153 young and 74 elderly participants (Babayan et al., 2019). To qualify as biomarker of cognitive decline, a second key aspect is the reliability of the aperiodic signal and the aperiodic-adjusted periodic activity. One recent study (Pathania, Schreiber, Miller, Euler, & Lohse, 2021) investigated the test-retest reliability (intraclass correlation, ICC) of the aperiodic slope in a sample of 60 healthy young adults. According to the general adopted interpretation of ICC (Cicchetti, 1994), excellent reliability measures on parietal and occipital electrode sites (.92 (parietal) and .90 (occipital)) were reported. Reliability of periodic signal components (i.e. aperiodic-adjusted power) were not addressed in this study. In contrast, a second previous study (Levin et al., 2020) investigated 22 children with Autism spectrum disorder (ASD) and 25 healthy children, and found poor reliability of the aperiodic slope (ICC = .28) for healthy children and good reliability (ICC = .70) for children with ASD. They further reported excellent reliability for alpha peak power in both subsamples (healthy: ICC = .86, ASD: ICC = .82). Thus, reliability of the aperiodic and aperiodic-adjusted signal
components demands further clarification. In the context of aging research, it is important to assess test-retest reliability of aperiodic and aperiodic-adjusted power measures within large scaled samples of both adults and older subjects. Adequate test-retest reliability is a prerequisite for longitudinal aging studies and for research on biomarkers of the aging brain. Reliability estimates represent the ratio of within-subject variance (i.e., the measurement error) to the between-subject variance (i.e., difference between age groups). The within subject variance may differ between populations and thus may not be applicable to the elderly population when measured in healthy young adults (Matheson, 2019). If the within-subject variance explains a large proportion of the total observed variance, drawing any conclusion about between-subject differences is precluded (Matheson, 2019). Neglecting reliability measures can thus result in costly studies that are unable to produce informative outcomes. Therefore, it is a fundamental requirement to estimate reliability for these newly emerging measures in the context of aging research.

In the current study, the test–retest reliability of the aperiodic intercept and slope and of the total and aperiodic-adjusted posterior alpha power were assessed. The sample of 100 young and 100 elderly individuals were used, from whom data was acquired at two consecutive measurements separated by a week.

Finally, the association between the decomposed power spectrum and cognitive functions were examined. Literature has established a link between age-related decline in total alpha power with diminished attention and working memory performance (Babiloni et al., 2006; Doppelmayr, Klimesch, Stadler, Pöllhuber, & Heine, 2002; Ishii et al., 2017; Klimesch, 1999; Klimesch, Vogt, & Doppelmayr, 1999; Polich, 1997; Scally et al., 2018). However, these well-established findings were challenged by demonstrating that age-related cognitive decline is linked to a flattening of the aperiodic signal (Voytek et al., 2015). Thus, it remains unclear to what extent this relationship between alpha power and cognitive performance is in fact confounded by the aperiodic slope. The present report specifically addressed the relation of resting state alpha power and cognitive abilities (Doppelmayr et al., 2002; Klimesch et al., 1999; Langer et al., 2012; Thatcher, North, & Biver, 2005). Therefore, neuropsychological tests assessing attention and working memory performance were conducted in this sample of 100 young and 100 elderly participants. Subsequently, relationships to the aperiodic signal components and the different measures of upper alpha power were examined, as previous studies found significant correlations with cognitive scores most consistently in the upper alpha band (Doppelmayr et al., 2002; Klimesch et al., 1999; Langer et al., 2012).

The analysis code for the present study was implemented in a pilot dataset (Langer, Bastian, Wirz, Oberauer, & Jäncke, 2013) before either of the two larger, independent datasets were accessed or analyzed. All relevant analysis parameters were fixed before conducting the main study, so there were no degrees of freedom in the planned analyses, and overfitting errors were minimized. Sequential Bayesian updating was employed by fitting a Bayesian regression model to each of the three datasets and passing posterior distributions of each analysis to the next analysis as priors. Thus, evidence could be accumulated across the datasets. This produced greater statistical power than independent analyses and more robust outcome parameters.

Based on previous literature and pilot data results, the present hypotheses were as follows:

- **H1a**: The alpha rhythm is slower (i.e., has lower alpha peak frequency) in the elderly group than in the young group.
- **H1b**: In the canonical, lower and upper alpha band, there is lower total power in the elderly group than in the young group.

The age differences in alpha power change when adjusting for the aperiodic signal:

- **H2a**: The upper and canonical alpha bands exhibit less age difference in aperiodic-adjusted alpha power than in total alpha power.
- **H2b**: The lower alpha band exhibits greater age difference in aperiodic-adjusted alpha power than in total alpha power.

Age differences in the aperiodic parameters were expected as follows:

- **H3a**: The aperiodic intercept is lower in the elderly group than in the young group.
- **H3b**: There is a flatter aperiodic signal (i.e., a smaller aperiodic exponent) in the elderly group than in the young group.

| Parameter of uncorrected (“total”) PSD | Parameter from aperiodic-adjusted PSD | Description |
|----------------------------------------|---------------------------------------|-------------|
| Total canonical alpha power            | Aperiodic-adjusted canonical alpha power | Averaged log power in 8–13 Hz window |
| Total lower alpha power                | Aperiodic-adjusted lower alpha power   | Averaged log power in window [-4 Hz IAF] |
| Total upper alpha power                | Aperiodic-adjusted upper alpha power   | Averaged log power in window [IAF +2 Hz] |
| Individual alpha frequency (IAF)      | Individual alpha frequency             | Frequency at maximum power in search window 7–14 Hz |
| N/A                                    | Aperiodic intercept                    | Intercept parameter of the aperiodic signal component |
| N/A                                    | Aperiodic exponent                     | Exponent parameter of the aperiodic signal component |

Note: Individual alpha frequency is not affected by the adjustment for the aperiodic signal. If the search criteria in the total power spectrum could not be met, IAF was also not be taken from the flattened (aperiodic-adjusted) power spectrum. Aperiodic intercept and exponent are not applicable on the uncorrected PSD.
With respect to the test-retest reliability:

- H4a: Both age groups exhibit a good to excellent test–retest reliability (i.e., ICC, >0.6) for the total and aperiodic-adjusted alpha parameters and for the aperiodic exponent and intercept.
- H4b: There are equivalent levels of test–retest reliability in the total and aperiodic-adjusted alpha parameters and in the aperiodic exponent and intercept in both age groups.

With respect to the relationship between cognitive scores and the different parieto-occipital alpha power and aperiodic signal measures:

- H5a: Total upper alpha power is positively related to attention and working memory performance.
- H5b: This relationship is weaker when applied to aperiodic-adjusted alpha power.
- H5c: The aperiodic signal exponent is positively related to attention and working memory performance.

Supplementary table A.1 summarizes each hypothesis and the statistical analyses that were performed to test them.

2. Methods

2.1. Datasets

This study used data that was recorded in our laboratory as part of a larger project while preparing the stage 1 submission. The larger project aims to quantify healthy-aging-related task performance and neuroelectric correlates in seven EEG tasks as well as in EEG resting-state recordings. The tasks aim to measure different cognitive functions such as working memory and processing speed. One hundred healthy elderly subjects (60–80 years) and 100 healthy young participants (18–35 years) were recruited. Exclusion criteria were suffering from psychiatric symptoms, severe neurological disorders such as epilepsy, prior head injuries, a stroke, a transient circulatory disorder of the brain, diagnosis of dementia, Huntington’s disease, Parkinson’s disease, current use of psychotropic drugs such as antidepressants, alpha-agonists, neuroleptics, and mood stabilizers, and intake of any recreational drugs. Additionally, subjects whose score in the mini-mental state examination (Folstein, Robins, & Helzer, 1983) (MMSE) was below 27 were excluded due to the high risk of dementia or mild cognitive impairment (O’Bryant et al., 2008). Each subject took part in two experimental sessions following the identical EEG protocol. This was done to assess the test–retest reliability of all dependent measures. The sessions were scheduled with an inter-session interval of one to two weeks and at the same time of the day. The local ethics committee has approved the project, and all participants gave their written informed consent to participate in the study. The present study analyzed resting-state EEG data of participants who took part in both recording sessions: 400 recordings of 200 participants.

Additionally, a second independent dataset served the validation of the results obtained in our laboratory. This openly available, published dataset (Babayan et al., 2019) contains resting-state EEG measurements of 215 healthy participants comprising a young and an elderly group (Nyoung = 153, mean age = 25.1 years, sd = 3.1, age range = 20–35 years, 45 female; Nold = 74, mean age = 67.6 years, sd = 4.7, age range = 59–77 years, 37 female). These two datasets had not been evaluated in any way and were analyzed only after in principle acceptance of the present manuscript.

A third dataset was used for the pilot analysis (see below). This dataset originates from a previous study (Langer et al., 2013) and contains EEG recordings of 118 subjects (Nyoung = 63, mean age = 23.37 years, sd = 3.91, age range = 18–35 years, 40 female; Nold = 55, mean age = 68.40 years, sd = 3.29, age range = 61–77 years, 23 female). More details about the pilot dataset are provided in Appendix B.

2.2. Experimental setup and procedure

Prior to the EEG assessment, participants performed a cognitive test battery. During EEG acquisition individuals were comfortably seated in a chair in a sound- and electrically shielded Faraday recording cage. The cage was equipped with a chinrest to minimize head movements and a 24-inch monitor displaying a fixation cross. Participants were informed that EEG is recorded while they rest with their eyes alternately open or closed. Instructions to open or close the eyes were automatically presented via cage intern loudspeakers. Adopting the recording protocol from previous studies (Alexander et al., 2017; Langer et al., 2013), within five repetitions, participants were asked to fixate for 20 sec followed by 40 sec of eyes closed recordings. This resulted in 100 s eyes open and 200 s eyes closed data available for further analysis. The MATLAB code used for this recording protocol is archived in an OSF repository (https://osf.io/8e2kd/).

2.3. Cognitive assessment

The cognitive assessment included the Trial making Test A/B (Lezak, Howieson, Loring, & Fischer, 2004) and digit span forward/backward task (Wechsler, 1997). Both tasks are extensively used in neuropsychological and aging research, and are among the most commonly applied tests in clinical practice as a measure of working memory performance (Camara, Nathan, & Puente, 2000). Numerous studies reported age related decline in performance in both the digit span task (Bopp & Verhaeghen, 2005, pp. P223–P233; Grégoire & van der Linden, 1997; Hester, R. L., Kinsella, G. J., & Ong, B., 2004; Monaco, Costa, Caltagirone, & Carlesimo, 2013; Myerson, Emery, White, & Hale, 2003) and the TMT A/B test (Cangoz, Karakoc, & Selekler, 2009; Giovagnoli et al., 1996; Goul & Brown, 1970; Hamdan and Hamdan, Eli Mara L. R., 2009; Kennedy, 1981; Rasmussen, Zonderman, Kawas, & Resnick, 1998; Tombaugh, 2004). Therefore, these task are highly eligible to capture age-related decline in working memory functions. Additionally, the digit span forward backward task is a subscale which was also employed by Thatcher et al. (2005), when relating resting state alpha power with intelligence.

2.3.1. TMT A/B task

In the TMT A task, the participant is asked to increasingly connect a series of 25 spatially distributed circled numbers...
using a pencil. In the B part, 25 circled numbers and letters need to be connected alternatingly in a numerical and alphabetical order. Time to completion is measured by the experimenter. The subtest TMT A measures motor speed and visuospatial attention, the B version further captures working memory operations such as executive control (Crowe, 1998; Sánchez-Cubillo, I., Periáñez, J. A., Adrover-Roig, D., Rodríguez-Sánchez, J. M., Rios-Lago, M., Tirapu, J. E. E. A., & Barceló, F., 2009). The score of the TMT A and B versions are defined as the time to completion in each condition. The ratio of TMT B/TMT A were calculated as a final score was related to the parameters of the decomposed power spectrum. This is thought to minimize visual attention components and to be a more direct indicator of working memory function (Misdraji & Gass, 2010).

2.3.2. Digit span task

The digit span task constitutes a forward and backwards version. A sequence of numbers is read to the participant who is then asked to repeat the sequence either forward or in reverse order. The length of the sequence increases until the participant fails to recall the correct order twice (Wechsler, 1997). The forward task is designed to measure attention and short term memory, or the functioning of the phonological loop component of Baddeley's working memory model (Baddeley, 2000). The digit span backwards task captures working memory processes such as executive control functions (Giofrè, Stoppa, Ferioli, Pazzuti, & Cornoldi, 2016; Hester, R. L., Kinsella, G. J., & Ong, B., 2004). Thus, only the digit backwards score was used as the outcome measures of interest. The performance score was defined as the number of correctly recalled sequences in each condition.

2.4. Electroencephalography acquisition and preprocessing

The high-density EEG was recorded at a sampling rate of 500 Hz, using a 128-channel EEG Geodesic Sensor Net system (Electrical Geodesics, Eugene, Oregon). The recording reference was at Cz (vertex of the head), and impedances were kept below 40 kΩ. All subsequent analyses were be performed using MATLAB 2018b (The MathWorks, Inc., Natick, Massachusetts, United States). EEG data were automatically preprocessed using the current version (2.5) of the MATLAB toolbox Automatic (Pedroni, Bahreini, & Langer, 2019). The analysis pipeline consisted of the following steps. First, error-prone channels were detected by the algorithms implemented in the eeglab plugin clean_rawdata (http://sccn.ucsd.edu/wiki/Plugin_list_process). An electrode was defined as an error-prone when recorded data from that electrode was correlated at less than .85 to an estimate based on neighboring electrodes. Furthermore, an electrode was defined as error-prone if it had more line noise relative to its signal than all other electrodes (4 standard deviations). Finally, if an electrode had a longer flat line than 5 s, it was considered error prone. These error-prone electrodes were removed automatically and later interpolated using a spherical spline interpolation (EEGLAB function eeg_interp.m). This interpolation was performed as a final step before the automatic quality assessment of the EEG files (see below). Next, data was filtered using a high-pass filter (cutoff frequency (-6 dB): .5 Hz) and Zapline (Cheveigné, 2020) was applied to remove line noise artifacts, removing 7 power line components. Subsequently, independent component analysis (ICA) was performed on temporary high-pass filtered data (cutoff frequency (-6 dB): 1 Hz). Components reflecting artifactual activity were classified by the pre-trained classifier ICLabel (Pion-Tonachini, Kreutz-Delgado, & ICLabel, 2019). Each component classified with a probability rating >.8 for any class of artifacts (line noise, channel noise, muscle activity, eye activity or heart artifacts) was removed from the data. The retained components were back-projected on the .5 Hz high-pass filtered data. Finally, residual bad electrodes were excluded if their standard deviation exceeded a threshold of 25 µV. After this, the pipeline automatically assessed the quality of the resulting EEG files based on four criteria. First, a data file was marked as bad-quality EEG and was not included in the analysis if the proportion of high-amplitude data points in the signals (≥30 µV) was larger than .2. Second, more than 20% of time points showed a variance larger than 15 µV across channels. Third, 30% of the electrodes showed high variance (≥15 µV). Fourth, the ratio of bad electrodes was higher than .3. This standardized and objective preprocessing pipeline and data quality metrics removed all degrees of freedom from the preprocessing. The analysis code for the performed preprocessing can be found in an OSF repository (https://osf.io/8ezkd/) and was applied on all three investigated datasets. After this automatic preprocessing step, the resulting continuous EEG data were down-sampled to 125 Hz, and the number of electrode were reduced to a subset of the 70 electrodes that closely match the standard 10-10 electrode locations (Luu & Ferree, 2000). This was done to reduce computational costs for parametrization of the neural power spectra and estimation of the Bayesian statistical models. It also allowed direct comparison of EEG from the three datasets using different cap layouts: ours described above, that of the validation dataset (Babayan et al., 2019) and that of the pilot dataset (Langer et al., 2013). Finally, the data was referenced to a common average reference. The first and the last 2 sec of each eyes-closed block were discarded to exclude motor activity related to opening and closing the eyes and auditory activity due to the prompt from the loudspeakers. The remaining data was concatenated, resulting in a total of 180 s of continuous EEG data. If a dataset contained less than 180 s of data due to technical errors (e.g., aborted measurement, missing triggers) the data file was excluded from further processing. Subsequently, the data was further segmented into epochs of 2 s length. EEG epochs exceeding a ±90uV amplitude threshold were excluded from further analysis. We note that, because several quality metrics from the Automagic toolbox were used for selecting EEG data, it was unlikely that at this point a significant number of EEG epochs would be excluded. Nevertheless, we excluded subjects from the analysis for whom less than 50% of the epochs for the eyes closed condition remained available for further analyses.

2.5. Spectral analysis

Spectral analysis was performed on artifact-free 2 sec segments from five blocks of the eyes-closed condition.
Only data from the eyes closed condition were analyzed, as this data contains fewer artifacts and generally shows the strongest alpha amplitudes. Additionally, eyes-closed data has been previously used to establish a link between age and alpha power (Babiloni et al., 2006; Breslau et al., 1989; Polich, 1997; Vysata et al., 2012). Power spectral densities (PSDs) were then calculated using Welch’s Method (Welch, 1967) as implemented in the EEGLab toolbox (Delorme & Makeig, 2004) (by default, non-overlapping windows). Zero padding was applied to provide a frequency resolution of .25 Hz in the 2 sec time windows. Averaging the individual PSDs of each window resulted in a smoothed power spectrum that complies with the requirements of the SpecParam algorithm used subsequently (see below, Fig. 1). Additionally, PSDs were transformed to log scale, to make results equally scaled to outputs from the SpecParam algorithm, which only operates in log space. In the following, the two approaches to extract total alpha power and the aperiodic-adjusted alpha power together with the aperiodic signal are described. Table 1 provides an overview of all extracted parameters.

2.5.1. Computation of total alpha power

In this standard analysis approach, no adjustment were made for the aperiodic signal, as it had been used throughout previous literature. First, the IAF was determined by extracting the maximum power value in between a lower and upper frequency limit (Klimesch, 1999). Following previous work, these frequencies limits were set to 7 and 14 Hz (Posthuma, Neale, Boomsma, & Geus, 2001; Smit, Wright, Hansell, Geffen, & Martin, 2006). If this maximum was at the border of the search range, no IAF was extracted for that subject and the corresponding data was excluded from further analysis (see also exclusion criteria in section 2.5.4). Therefore, the effective search range for the IAF was between 7.5 and 13.5 Hz. If an IAF could be identified, additional alpha sub-bands were extracted: total lower alpha power [−4 Hz IAF] and total upper alpha power [IAF +2 Hz] were calculated by averaging power in the above-defined range in reference to the IAF (Klimesch, 1999). Additionally, the commonly used total canonical alpha band power was calculated by averaging power in the range fixed of 8–13 Hz (Babiloni et al., 2006).

2.5.2. SpecParam algorithm

The SpecParam algorithm (Donoghue, Haller, et al., 2020) parameterizes the power spectrum to separate oscillations from the aperiodic signal. The algorithm estimates oscillatory peaks that are superimposed on the aperiodic signal (see Fig. 1) and therefore measured relative to this rather than to the absolute zero. Thus, it parameterizes the PSD by iteratively fitting the aperiodic signal (L) to the observed smoothed spectral signal, resulting in two parameters: the aperiodic intercept b and the aperiodic exponent c (i.e., negative slope, the smaller c, the flatter the spectrum).

\[ L = b - \log(k + F^c) \]

Here, F represents the vector of input frequencies and k the “knee” parameter, which is not further discussed here, as it is set to 0 in the proposed analysis (i.e., no bend of the aperiodic component is additionally modeled in the data, which is the default state of the SpecParam algorithm).

In order to extract oscillatory components, this aperiodic signal is subtracted from the power spectrum. Gaussians are iteratively fitted to the remaining signal and subsequently subtracted whenever data points exceed two standard deviations of the data. The Gaussians represent the true oscillatory components in the data; if data points are below the specified threshold, they are considered as noise. This results in a data-driven number of Gaussians, each parameterized by the frequency center, power relative to the aperiodic signal and the frequency bandwidth. The power spectrum is therefore modeled by

\[ P = L + \sum_{n=0}^{N} G_n + \epsilon, \]

where \( G_n \) represents the nth Gaussian, and \( \epsilon \) the noise not captured by the model. Note that this description of the algorithm is simplified; for a more detailed definition, see ref (Donoghue, Haller, et al., 2020).

In the performed analyses, the frequency range of 2–40 Hz was passed to the algorithm because very low frequencies may lead to overfitting of noise as small bandwidth peaks. The release 1.0.0 of the SpecParam toolbox from the github repository (https://github.com/fooof-tools/fooof) was used. The following settings for the algorithm were applied: peak width limits: [1, 8]; max number of peaks: infinite; minimum peak height: 0; peak threshold: 2 sd above mean; and aperiodic mode: fixed.

To correct the above-described total alpha power measures (see 2.5.3) for the aperiodic signal, the aperiodic signal was reconstructed by its parameters. Subsequently, the aperiodic signal was subtracted from the total power spectrum to receive an aperiodic-adjusted power spectrum. Using this power spectrum, aperiodic-adjusted alpha power values (aperiodic-adjusted canonical alpha power, aperiodic-adjusted lower alpha power, aperiodic-adjusted upper alpha power) were calculated in the frequency ranges described above (2.5.1).

2.5.3. Cluster-wise analysis

To test age effects in electrode sites derived from literature, electrode-cluster-based analyses were performed. This cluster was based on data from the parietal and occipital electrodes: E72 (P0z), E75 (Oz), E62 (Pz), E67 (P03), E77 (P04), here referred to as the parieto-occipital cluster (see Fig. 3a). These electrodes were chosen because of the strong prominence of Oz and Pz electrodes in EEG alpha peak research (Klimesch, 1999) and previous findings for age effects on alpha band power in these electrodes (Breslau et al., 1989; Polich, 1997). To account for individual anatomical differences and to create a more robust cluster, the three electrodes adjacent to Oz (E75) and Pz (E62) were added (E72 (P0z), E67 (P03), E77 (P04)). All the parameters described above were averaged within the cluster.

2.5.4. Exclusion criteria

A data file was be processed if any of the criteria applies (see 2.4).

- The file was marked as bad quality EEG by the Automagic preprocessing pipeline.
The file did not contain 180 s of eyes closed resting state EEG data (due to technical errors such as missing triggers or aborted measurements).

50% of the segmented data got rejected due to high amplitude time points ($\pm 90\mu V$)

Before statistical analyses were performed, data was excluded if any of the following criteria applies.

- The fit of the parameterized power spectrum to the original PSD was below a cut-off of $R^2 < .9$. If the fit of the parameterized spectrum was below the specified cut off, total alpha parameters were still included, as these are not contingent on the parametrization of the SpecParam algorithm.
- Any of the extracted parameters exceeded a threshold of 3 standard deviations above or below the mean of the sample.
- No individual alpha peak could be detected. If no alpha peak could be detected, aperiodic signal components of the according subject were still used, as the aperiodic signal components do not depend on the individual alpha peak detection.

These three criteria were applied within data of each electrode separately.

### 2.6. Statistical analyses of age differences

Bootstrapping statistics were conducted on each dataset individually, and to accumulate evidence across datasets, multivariate Bayesian generalized linear mixed models were applied. To correct for multiple comparisons in the statistical analyses, the significance level was adjusted. We assumed a high correlation between the nine outcome variables, as many of the dependent variables represent different characteristics of the individual alpha oscillations. To account for this, we first calculated the effective number of tests of all dependent variables using Nyholt's approach (Nyholt, 2004). Following this approach, the significance level (.05) was then adjusted using Sidak-Correction (Nyholt, 2004). Subsequently, the confidence intervals of the bootstrap statistics (see 2.6.1) as well as the credible intervals (CIs) of the Bayesian posterior distributions (see 2.6.2) were defined based on the newly calculated levels of significance.

Besides the electrode cluster based analysis, we also investigated the spatial distribution of all statistical parameters on full scalp level. To correct for multiple comparisons we applied a non-parametric cluster-based permutation analysis. This was planned to be done using the ft_drewestatistics function implemented in FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) (see 3.1 for deviations of this plan).

#### 2.6.1. Bootstrap analysis

For each dataset, robust and assumption free bootstrap statistics were performed. Therefore the original data was permuted 10,000 times. To investigate age effects within each of the nine above-described parameters (see Table 1), the mean age differences of all nine parameters were calculated within each permuted dataset. Subsequently, the corrected confidence interval of the bootstrapped age differences were calculated for each measure. If this interval did not include zero, the age difference were considered significant.

#### 2.6.2. Bayesian regression model

In order to accumulate evidence across the three different dataset used in this study, an additional multivariate Bayesian generalized linear mixed model was formulated using the brms (Bayesian Regression Models using ‘Stan’) R package (Bürkner, 2017). In this analysis, the model was fitted to the pilot data, using uninformative priors (see below). The extracted posteriors were not interpreted but used as priors for the next analysis of the main dataset ($N = 200$), which used the same model as before. This was done by applying the best fitting distribution to the posterior samples using the fitdistrplus R package (Delignette-Muller and Dutang, 2015). The resulting posterior distributions of the main analyses were approximated the same way and then served as priors for the analyses of the validation dataset (Babayan et al., 2019) ($N = 215$). Only these resulting posterior distributions of the age effects were interpreted as a final and more robust outcome.

The multivariate model was chosen as it is able to account for correlations between multiple dependent variables. Further advantages of this Bayesian approach are the facilitations to make inferences about the nonexistence of any effects and to statistically compare posterior distributions of the different parameters. In all performed analyses, the following model was used. To account for the repeated measurement structure of the study design of the main analysis (two identical measurements of each subject within 1–2 weeks) and the multiple dependent variables per subject, random intercepts were added for the participant IDs as shown in equation 1:

$$[	ext{d}u/s] \sim \alpha_{\text{group}} + (1 | \text{participantID})$$

This model was fitted five times in each of the three datasets: for each of the three alpha band power parameters together with their according aperiodic-adjusted equivalent (lower alpha, upper alpha, canonical alpha), for the aperiodic signal components together (intercept and exponent) and for the IAF. This allowed the direct comparison between the resulting posteriors of each total alpha parameter and its corresponding aperiodic-adjusted equivalent using the brms hypothesis function (see below).

If the corrected posterior CI of a parameter of the model did not include 0, it was considered significant. This allowed to test hypotheses H1a, H1b, H3a and H3b. If the CI included zero, the test for practical equivalence (Kruschke, 2014, 2018) was used to assess whether the observed effect was in favor of the null hypothesis. The test for practical equivalence is based on the “HDI + ROPE” decision rule (Kruschke, 2014, 2018) to decide whether parameter values should be accepted or rejected against an explicitly formulated null hypothesis (i.e., region of practical equivalence “ROPE”). If the ROPE completely covers the 89% highest density interval (HDI, i.e., credible values of a parameter are inside the ROPE) the null hypothesis is accepted. According to the recommendation by Kruschke (2018), the ROPE was set to a negligible effect size ($d = -.1$ to $d = .1$) (Cohen, 1988). Converting this effect size to the betas provided by the
models (standard deviation of the dependent variable is .5, see below), yielded a ROPE of \(-.05\) to \(.05\) (Lipsey & Wilson, 2009).

Furthermore, to test whether age differences were changing when adjusting alpha parameters for the aperiodic signal (H2a & H2b), the according posterior distributions were compared. Therefore, one sided Bayes Factors were calculated for the hypotheses total alpha power age effect parameter \(>\) aperiodic-adjusted alpha power age effect parameter or total alpha power age effect parameter \(<\) aperiodic-adjusted alpha power age effect parameter, depending on the corresponding above-described hypotheses H2a and H2b. This was done using the brms hypothesis function (Bürkner, 2017).

Additionally, to estimate how strongly the age differences change, Cohens’s d was calculated and reported for the age differences within each alpha measure.

In line with recommendations by Gelman, Jakulin, Pittau, and Su (2008) for Bayesian regression models, the predictors and outcome variables were scaled as follows: The binary parameter (age) was centered at 0 and each numeric parameter (total canonical alpha power, aperiodic-adjusted canonical alpha power, individual alpha frequency, aperiodic signal exponent and aperiodic signal intercept) was scaled to provide a mean of 0 and standard deviation .5. For the first analysis of the pilot data, weakly informative Cauchy priors (mean = 0, scale = 2.6.2) were chosen in line with recommendations (Gelman et al., 2008) for Bayesian regression models.

2.7. Source level analysis

To investigate the neural generators of aperiodic-adjusted alpha power and aperiodic exponent, source level analysis utilizing a beamformer spatial filtering approach were applied. A template forward model was derived from the MNI ICBM 2009 template brain (http://www.bic.mni.mcgill.ca/ServicesAtlases/ICBM152Nlin2009) using the OpenMEEG implementation (Gramfort, Papadopoulo, Olivi, & Clerc, 2010) of the Boundary Element Method (REM). The linear constrained minimum variance (van Veen, van Drongelen, Yuchtman, & Suzuki, 1997) (LCMV) beamformer algorithm was applied to construct the spatial filters. These spatial filters were then be multiplied with the eyes closed time series data, resulting in source level time series for each voxel. Subsequently, source power spectra were calculated and decomposed into aperiodic and periodic signal components as described in 2.5. Based on these, aperiodic-adjusted canonical alpha power and the aperiodic exponent parameter were visualized.

2.8. Test-retest reliability

In order to quantify test–retest reliability for the output measures collected at the two recording sessions per subject, we calculated one-way random-effects model intraclass correlation coefficients. This was done using the absolute difference (Earthman, 2015; Sedgwick, 2013). The equivalence test seeks to determine whether the reliability difference between the two groups or conditions is at least as extreme as the smallest effect size of interest (SESOI), following the two one-sided tests (TOST) procedure. In other words, the equivalence test does not test whether there exist no reliability differences at all between the groups. Rather does it examine whether the hypothesis, stating that reliability differences are extreme enough to be considered meaningful, can be rejected (Lakens et al., 2018). Performing TOST therefore involves determining the SESOI. Thus, SESOI and its lower and higher equivalence bounds respectively need to be determined first. As ICC values can be roughly compared to Cohen’s d effect size measures, we considered an ICC of \(+ .1\) as the respective equivalence bounds. The TOST procedure was then planned to be performed against lower and upper equivalence bounds that are specified based on the SESOI.

2.8.1. Equivalence test

To test hypotheses 5a, 5b and 5c, Spearman correlations between the different measures of parieto-occipital upper alpha power and the aperiodic signal (total and aperiodic-adjusted upper alpha power, aperiodic exponent and intercept) and the TMT B / TMT A and the digit span backwards score were calculated. The upper alpha band was selected because previous studies found significant correlations with cognitive scores especially in the upper alpha band (Doppelmayr et al., 2002; Klimesch et al., 1999; Langer et al., 2012).

Spearman correlation was preferred over Pearson correlation to avoid effects of outliers and to minimize bias due to possible non-normality of the data. To test hypothesis 5b, we tested whether correlation coefficients between aperiodic-adjusted alpha power measures and the cognitive scores are smaller than correlation coefficients between total alpha power measures and the cognitive scores. Therefore, a confidence interval based one sided test for dependent, overlapping
correlation coefficients implemented in the R cocor package (Diedenhofen & Musch, 2015) was be applied (Zou, 2007). Equivalence tests were additionally performed as described in 2.8.1. SEOSI was be defined as $r = .1$, which is the smallest correlation coefficient acknowledged as a meaningful effect by Cohen (1962). This procedure was applied to data of the young and elderly group separately.

### 2.10. Power analysis

In order to determine statistical power in the available sample, a literature search was conducted. Subsequently, a simulation-based power analysis was performed. The literature search focused on age differences in the following EEG features: spectral power in the alpha frequency range as well as parameters extracted by the SpecParam algorithm (i.e., aperiodic signal exponent and intercept). Five studies were identified which reported analyses similar to the planned analyses on age differences in total alpha power (Babiloni et al., 2006; Breslau et al., 1989; Polich, 1997; Roubicek, 1977; Vysata et al., 2012).

Roubicek (1977) reported a $P$-value ($P < .01$) but no measure that could be used to calculate an effect size. Breslau et al. (1989) reported $t$-values of interest as a topographical plot in which the color scale represented individual $t$-values. From this color scale, no exact values can be extracted for further calculation. Vysata et al. (2012) provide unstandardized regression coefficients but these do not allow any calculation of an effect size. The remaining two studies (Babiloni et al., 2006; Polich, 1997) both divided the alpha band into a lower and an upper sub-band. Polich (1997) reported a negative correlation of $r = -.27$ between upper alpha band power and age in a parietal electrode (Pz). Babiloni et al. (2006) calculated alpha power on source space. The upper alpha band was investigated in the occipital and parietal brain regions which most closely match the electrode cluster in the planned study. For the occipital cluster, an $r^2$ of $.18$ ($r = \pm .42$) was reported; for the parietal cluster, the corresponding $r^2$ value was $.1$ ($r = \pm .32$). Taken together, the literature review revealed five studies reporting consistent age differences in total alpha power, but only two allowed a calculation of effect sizes. Due to the small number of available observations and the high probability of publication bias (e.g., Franco, Malhotra, & Simonovits, 2016), only the smallest observed effect ($r = -.27$) was chosen as the basis for power analysis. This value was transformed to Cohen’s $d$, resulting in $d = .56$.

The literature search for age differences in resting state aperiodic signal parameters yielded three studies. Voytek et al. (2015) reported a correlation of aperiodic signal slope with age of $r = .66$ ($d = 1.75$). Donoghue, Haller, et al. (2020) found age differences of $d = 2.45$ for the aperiodic offset and $d = 2.63$ for the aperiodic exponent. In Thuwal et al. (2021) correlational analyses between age and aperiodic signal components yielded $r = -.47$ ($d = 1.07$) for the aperiodic offset, and $r = .82$ ($d = 2.86$) for the aperiodic slope (i.e. negative aperiodic exponent). Therefore, we conclude that the minimum sample size needed here is driven by the age differences in total alpha power ($d = .56$), as all other effects are larger and therefore require smaller sample sizes.

Next, a retrospective power analysis was performed, as the maximum number of participants available for the main study is 200. Therefore, a simulation-based approach was chosen. One thousand simulated datasets of alpha parameters were drawn randomly from normal distributions, each with a group difference of $d = .56$. On each dataset, a brms model was fitted investigating age effects on the alpha power. When the 98% CI of the model coefficient of the age effect did not include zero, the result was considered significant (Barret, 2019, July 21; Kruschke, 2014). When using a sample size of 200, the age effect was found in 93.8% of the 1000 simulations. Fig. 2 shows the results of the simulations using sample sizes ranging from 2 to 200.

Based on this simulation analysis, we conclude that the planned sample size of 200 subjects for the main analysis provides sufficient power for the investigation of both total alpha power and aperiodic signal parameters, even in the case of a considerable proportion of subjects drop out (see Fig. 2). This also applies to the validation dataset, which consists of data from 215 subjects.

For the relationship between resting state alpha power and cognitive abilities, four studies were identified. Thatcher et al. (2005) reported consistent positive associations between alpha power and Wechsler Intelligence Scale (Wechsler, 1997) scores, however, the correlation coefficients were not

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**Fig. 2** – Percentage of simulations (1000 per sample size) being sufficiently powered (i.e., showing significant age effects on total alpha power). Red line indicates power of .9.
reported. Langer et al. (2012) reported a correlation of $r = .36$ ($d = .75$) between total alpha power and cognitive abilities (here, psychometric intelligence, operationalized by the Ravens Advanced Progressive Matrices (Raven & Court, 1985). The two other identified studies (Doppelmayr et al., 2002; Klimesch, 1999) provided correlations between working memory performance (Klimesch et al., 1999) and intelligence (Doppelmayr et al., 2002): Intelligence Structure Test (IST), Baumlner (1974) and the Learning and Memory Test (LGT-3), Amthauer (1973)) graphically as bar plots, indicating similar or higher correlation coefficients in parietal and occipital electrodes. Power analysis for correlation coefficients was performed using the “pwr” R package (Champely et al., 2017). Parameters were set as: $r = .36$, $a = .02$ and power = .90. For the one sided hypothesis ($r$ greater than zero), the resulting sample size was 80. Thus, the here used sample provides sufficient power to test the relationship between resting state alpha power and cognitive abilities.

### 2.11. Secondary analyses

In order to validate the results obtained for the main dataset in the analysis described above, the same analyses were performed on an openly available dataset (Babayan et al., 2019). The dataset had been downloaded and no further observations on this data had been made before in principle acceptance of the manuscript. The dataset consists of EEG recordings of 215 healthy participants comprising a young and an elderly group. In this study, participants were seated in a sound-attenuated Faraday cage, a 16-min resting-state EEG was recorded (eight blocks of eyes-open condition, eight blocks of eyes-closed condition, each 60s long). EEG was recorded using 62-channel active ActiCAP electrodes, attached according to the international 10-10 system. Data was recorded with a sampling rate of 2500 Hz and referenced to the electrode FCz. Data was bandpass filtered between .015 Hz and 1 KHz, and impedances were kept below 5 KΩ.

To ensure that this data is comparable to that in the other two datasets, it was down-sampled to 125 Hz and only the first five of the eight eyes-closed blocks were used. We extracted data from a time-window ranging from 2 s to 38 s after the beginning of each block, as done with the main dataset. Data were preprocessed, analyzed, and scaled in exactly the same way as described above. Accordingly, the same exclusion criteria were applied.

For the remaining data, the same statistical procedure was applied here as described in 2.6.

As this dataset is publicly available it has been analyzed several times, yet no other study so far has done similar efforts to investigate EEG age differences in total or aperiodic-adjusted alpha power.

### 2.12. Outcome-neutral tests, feasibility checks, & bias minimization

In order to ensure that the obtained results can test the stated hypothesis, we performed quality checks and outcome-neutral tests. Data quality of the EEG recordings were automatically and objectively rated by the preprocessing pipeline. Datasets rated as insufficient quality were not included in further analysis (see 2.4). We further defined two neutral outcome conditions to verify the quality of the data. First, the grand average topographical distribution of total and aperiodic-adjusted alpha power were plotted. These plots indicated, whether alpha power shows the typically observed and well replicated topographical distribution, with maximum power in posterior and occipital electrodes (e.g., Breslau et al., 1989; Markand, 1990). For the second outcome neutral test, we investigated age differences in total alpha power, which is a prerequisite for testing whether these effects change when adjusting for the aperiodic signal. Repeating the robust previous findings of age related decreases in total alpha power (Babiloni et al., 2006; Breslau et al., 1989; Polich, 1997; Roubicek, 1977; Scally et al., 2018; Vysata et al., 2012) ensured that the data is of high quality and can therefore be employed to test the additional hypothesis.

Pilot analyses (see Appendix B) served as feasibility checks for the analysis code, i.e., as descriptive support for the principled evaluation of the proposed hypotheses. Positive controls, as defined for classical experiments, cannot be applied here, as no experimental manipulation is performed in resting state recordings.

All analysis code was prepared using the pilot sample and is shared in an OSF repository (https://osf.io/8e2kd/). The only changes for the analysis of the two main datasets, which had not been observed in any way so far, were done in order to adjust the scripts to correctly handle the different data structure of the two datasets. Additionally, blinding of the experimenter was introduced. For any age related analyses, age labels were shuffled until all analysis scripts were adapted to the new data and only revealed when the analyses were adapted to the new data. For the analyses on the relation of periodic and aperiodic signal components with working memory scores, we shuffled the working memory scores accordingly, until all scripts are adapted. This removed all the degrees of freedom for the experimenter.

### 2.13. Anticipated timeline

Data collection of the dataset recorded in our laboratory was ongoing at the time of submission of the stage 1 manuscript and expected to be completed within three months. Preprocessing, analysis and preparation of stage 2 submission including possible exploratory analysis were expected to be finished within five months after in principle acceptance.

### 2.14. Data availability plan

All data used for the planned analysis is stored on the OSF repository https://osf.io/8e2kd/. Only the pilot data (which are not part of the here reported preregistered analysis) cannot be shared, because they were collected previously without obtaining consent of the participants to further share their data. However, to exactly replicate the here presented results of the combined Bayesian analysis, the informative prior distributions (obtained from the Bayesian regression analysis on the pilot data) are shared in the repository. Furthermore, this repository contains code of the pilot analyses and the adapted analyses for the main dataset and the validation dataset. Additionally this repository contains the laboratory logs.
2.15. Ethical approval plan

The study was approved by the ethics committee of the canton of Zurich, Switzerland (BASEC-Nr: 2017–00226) and written informed consent was obtained from each subject.

3. Results

In the main dataset, 100 old subjects and 104 young subjects completed both recording sessions. One old subject was excluded as it exceeded the defined age range of the present study (60–80 years). Due to technical errors, four recording files were corrupt and could not be further processed. Five recordings were not used for further processing because less than 180s of EC data were available. Finally, eight files were excluded as they were rated as bad EEG data quality by the preprocessing pipeline. In all recordings, less than 50% of the 2s data segments exceed a threshold of ±90 μV, thus no data was excluded based on this criterion. This yielded a final sample size of 199 recordings of 103 young subjects and 190 recordings of 98 old subjects. Table 2 summarizes the final sample characteristics. For the specific analysis of test-retest reliability, 96 young subjects and 92 old subjects could be used, for which EEG recordings were available at both measurement time points.

Due to bad SpecParam model fits ($R^2 < .90$), 1.49% of data points were excluded in the group of old subjects, in the young group, 2% of data points were excluded (i.e., as described in 2.5.4: only the affected measures of the affected electrode was excluded, not the full subject). In the remaining data, both age groups showed a high model fit over all electrodes for the parameterized power spectrum ($R^2_{old} = .984$, $sd = .013$; $R^2_{young} = .989$, $sd = .008$).

Additionally, in the group of old subjects, 2.2% of data points were excluded as they exceeded a threshold of three standard deviations in any of the parameters; in the young group, 1.4% were excluded from further processing. Finally, because no IAF could be extracted, 1.9% of data points of the old subjects were excluded, and 2.7% in the young subjects.

Of the 215 retrieved resting state EEG files of the LEMON validation dataset, one recording file could not be read in Matlab and was excluded from further processing. Five subjects were excluded as they did not fit the defined age groups of the main dataset (age was between 35 and 60 years). In three recordings, there were missing triggers, thus, less than 180 s data could be extracted. These files were not used in further analyses. Two files were excluded as they were rated as bad EEG data quality by the preprocessing pipeline. Finally, one recording was excluded as more than 50% of the 2s data segments exceeded a threshold of ±90 μV. This yielded a final sample size of 208 subjects (see Table 2 for detailed final sample characteristics). Due to bad model fits ($R^2 < .90$), 2.22% of data points were excluded in the group of old subjects, in the young group, 2% of data points were excluded. In the remaining data, both age groups showed highly similar model fits as compared to the main dataset ($R^2_{old} = .981, sd = .013$; $R^2_{young} = .987, sd = .008$). Subsequently, 1.5% of data points were excluded because they exceeded a threshold of three standard deviations in any of the parameters in the group of old subjects, and 1.7% in the young group. Finally, 1.2% of data points of the old subjects were excluded and 4.1% in the young subjects as no IAF could be extracted.

Here, the results of the main and validation datasets will be presented, in the course of readability, results of the pilot sample are presented in Appendix B.

3.1. Deviations from the preregistered analysis plan

All analyses were performed as defined in the approved preregistered protocol (https://osf.io/fb6pc, repository also contains the unchanged Stage 1 manuscript), however, two adjustments had to be made which are described in the following. The first deviation from the preregistered analysis plan had to be made in the full scalp analysis of the Bayesian regression model (reported in section 3.3.1). We originally planned to apply cluster-based permutation tests to correct for the multiple comparisons across the electrodes using the ft_freqstatistics function implemented in fieldtrip. However, this requires to refit the brms models with permuted data 1000 times, for each electrode and for both datasets. Fitting the brms models of one electrode takes approximately 7.5 min, summing up in total to a computation time of approximately 1.85 years. Attempts to cut down computation time significantly by parallelizing this analysis (including calling the R brms scripts from the Matlab based fieldtrip toolbox functions) failed. Therefore, the scalp distributions of the beta estimates of the Bayesian regression models of each electrode are plotted, and significance is assessed by using the same significance level ($a = .0091$) as for the parieto-occipital electrode cluster analysis. However, the preregistered cluster-based permutation tests were performed in the additional analyses investigating each dataset separately, using t-test to test to determine differences between the age groups. Significance levels of the cluster based permutation test analyses were set in accordance with the Bayesian regression model, controlling for the effective number of tested outcome variables (i.e., $a = .0091$). Because this cluster-based permutation
test was based on independent t-tests, in the main dataset only T1 data was used.

The second deviation from the planned analysis refers to the equivalence tests which were performed to investigate whether old and young subjects show equivalent levels of test-retest reliabilities (ICC) in the periodic and aperiodic EEG parameters (reported in section 3.5.1). The original analysis plan stated that this will be done using the TOST R package, which is based on means and standard deviations of group differences. However, this cannot be applied to ICC values, which are single point estimates and provide no distribution of which the mean and standard deviation can be extracted. To estimate a distribution of ICCs, we implemented a bootstrap analysis. In this alternative approach, data of each age group was resampled 1000 times and the corresponding ICC values for each bootstrapped age group were calculated. The corresponding age difference in ICC within each iteration of the bootstrap analysis was then saved to obtain the distribution of age differences in the ICC. If the 90% confidence interval of this distribution fell completely within the predefined equivalence bounds, it was considered significant (i.e. equivalent).

Note that the young group was slightly oversampled (104 instead of 100 subjects) because the dropout rate was lower than expected.

3.2. Parieto-occipital electrode cluster

To test the hypotheses (1–5) derived from literature, the averaged periodic and aperiodic activity of the parieto-occipital electrode cluster was investigated. The total and aperiodic-adjusted power spectra and the aperiodic component of the parieto-occipital electrode cluster are depicted for each group separately in Fig. 3.

3.2.1. Combined Bayesian regression analysis

The primary findings in the present report are based on the Bayesian regression models. These models combined evidence across the three investigated datasets (pilot dataset, main dataset and validation dataset) to produce the most robust research outcomes.

The combined Bayesian regression analysis revealed a significant age-related slowing of the IAF (see Table 3). In the total alpha power measures, significant age-related decreases were observed in the canonical alpha band, as well as in the individualized lower and upper alpha band. After adjusting power for the aperiodic signal, the observed age effects were also significant, but the magnitudes of the effects were considerably smaller in the canonical and the upper alpha band (see Table 3 for detailed results). Accordingly, there was strong evidence that age effects on aperiodic-adjusted alpha power were smaller as compared to total alpha power in the canonical alpha band (BF = 23.24), the upper alpha band (BF = 10.99), but not in the lower alpha band (BF = .31). Fig. 4A illustrates the posterior distributions of the age effects on total and aperiodic-adjusted power. The aperiodic signal showed significant age-related decreases of its intercept and exponent (see Table 3 for a summary of all statistical results and supplementary figure A.1 in Appendix A for an illustration of the corresponding posterior distributions). Fig. 3 further illustrates maturational changes in the aperiodic signal. Adhering to the preregistered analysis protocol, no

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**Fig. 3** – Grand average spectral decompositions in parieto-occipital electrode cluster for both age groups in the main dataset (A) and the validation dataset (B). Shaded areas represent standard errors. Schematic head plots on the right illustrate the locations of the parieto-occipital electrode cluster for each dataset.
Table 3 — Overview of statistical results of age on the different periodic and aperiodic parameters in the parieto-occipital electrode cluster.

| Parameter                                      | Combined Bayesian regression: \( \beta_{\text{age}} \) (CI) | Main dataset: Bootstrapped age differences (CI) | Validation dataset: Bootstrapped age differences (CI) |
|-----------------------------------------------|-----------------------------------------------------------|-------------------------------------------------|-----------------------------------------------------|
| Individual alpha frequency                    | \(-.16 (-.21, -.10)\)                                    | \(-.62 (-.87, -.37)\)                         | \(-.45 (-.75, -.16)\)                               |
| Total canonical alpha power                   | \(-.12 (-.17, -.06)\)                                    | \(-.25 (-.36, -.12)\)                         | \(-.28 (-.47, -.10)\)                               |
| Aperiodic-adjusted canonical alpha power      | \(-.06 (-.12, -.01)\)                                    | \(-.14 (-.22, -.04)\)                         | \(-.13 (-.26, -.00*)\)                              |
| Total lower alpha power                       | \(-.13 (-.18, -.07)\)                                    | \(-.29 (-.42, -.15)\)                         | \(-.35 (-.56, -.14)\)                               |
| Aperiodic-adjusted lower alpha power          | \(-.11 (-.17, -.05)\)                                    | \(-.21 (-.32, -.11)\)                         | \(-.20 (-.35, -.04)\)                               |
| Total upper alpha power                       | \(-.11 (-.16, -.04)\)                                    | \(-.28 (-.43, -.12)\)                         | \(-.36 (-.59, -.12)\)                               |
| Aperiodic-adjusted upper alpha power          | \(-.06 (-.12, -.01)\)                                    | \(-.21 (-.34, -.08)\)                         | \(-.23 (-.42, -.04)\)                               |
| Aperiodic intercept                           | \(-.23 (-.27, -.18)\)                                    | \(-.34 (-.45, -.245)\)                        | \(-.52 (-.67, -.37)\)                               |
| Aperiodic exponent                            | \(-.23 (-.28, -.18)\)                                    | \(-.24 (-.306, -.17)\)                        | \(-.36 (-.45, -.27)\)                               |

Note: In the combined Bayesian regression, CI refers to the 99.1% credible interval; in the bootstrapped age differences to the 99.1% confidence intervals. *The exact value of the upper bound of the CI is 0.00013.

Fig. 4 — Visualization of statistical age differences in total and aperiodic-adjusted power in the three different measures of the alpha band of the parieto-occipital electrode cluster. Row A visualizes posterior distributions of the estimates of age on alpha power combining the pilot, the main and the validation dataset in the Bayesian regression analysis. For the analysis of the individual datasets (B: main dataset, C: validation dataset) distributions of the bootstrapped age differences are plotted. Schematic heads on the right indicate location of the parieto-occipital electrodes of which data was averaged.
additional equivalence tests were performed, as all investigated models showed significant age effects. Exploratory control analyses controlling for the unbalanced distribution of gender in the two investigated samples yielded highly consistent results (see exploratory analysis section 4.1 and supplementary table A.2 in Appendix A).

|                | Canonical band |             | Lower band |             | Upper band |
|----------------|----------------|-------------|------------|-------------|------------|
|                | Total          | Aperiodic-adjusted | Total | Aperiodic-adjusted | Total | Aperiodic-adjusted |
| Main dataset   | .53            | .41         | .54        | .54         | .64        | .44         |
| Validation dataset | .63            | .39         | .68        | .54         | .64        | .54         |

**Table 4** – Age differences (Cohen’s d) in the total and aperiodic-adjusted measures of alpha power in the main and the validation dataset.

![Graph](image)

**Fig. 5** – Scalp distribution of age related changes for total and aperiodic-adjusted canonical alpha power and the individual alpha frequency. Cold colors indicate age related decreases. A: Results of the combined Bayesian regression analysis. Beta estimates for the age effect on each parameter are plotted across the scalp. Electrodes showing significant age effects (99.1% Credible interval does not include zero) are highlighted in yellow. B: Age group differences assessed by Cohen’s d in the main dataset. Above each difference plot, topographies of the corresponding measures are plotted for each age group. Electrodes showing significant age differences in the cluster-based permutation statistics are highlighted in yellow. C: Same visualization for the validation dataset.
3.2.2. Single dataset analysis

To investigate whether there were notable differences across the datasets that were combined in the Bayesian regression analysis, additional analyses for the parieto-occipital electrode cluster were performed separately on the main and the validation dataset. Results on both datasets were largely consistent to those obtained in the Bayesian regression analysis.

The Bootstrap analysis replicated the age-related slowing of the alpha frequency, the decrease of the aperiodic intercept and the flattening of the aperiodic slope (i.e. decreased aperiodic exponent) in parieto-occipital electrodes both datasets. In line with the Bayesian regression results, total measures of parieto-occipital alpha power (canonical, upper and lower) showed significant age related decreases in the main and the validation datasets (see Table 3 and Fig. 4B and C). Also aperiodic-adjusted lower and upper alpha power showed consistent significant age-related decreases across datasets. Cohens d's indicate that age differences in aperiodic-adjusted alpha power tend to be smaller as compared to total alpha power (see Table 4).

3.3. Full scalp analysis

To additionally investigate whether age effects are observed outside the predefined region of interest (i.e. parieto-occipital electrode cluster), which was based on previous literature, full scalp analyses were performed.

3.3.1. Combined Bayesian regression analysis

The Bayesian regression model indicated that the observed age-related decreases in the IAF, the aperiodic intercept and the aperiodic exponent were not specific to the parieto-occipital electrode cluster, but were significant in all electrodes across the scalp (applying the same significance level as in the analysis of the parieto-occipital electrode cluster analyses, see Figs. 5A
Performing cluster-based permutation tests to beta estimates of the Bayesian regression model is computationally not feasible (see 3.1), instead we conducted the cluster-based permutation test based on t-tests for the analysis of the individual datasets (see 3.3.2). In total alpha power, age effects showed highly consistent spatial patterns in the canonical, lower and upper alpha band: The Bayesian models provided evidence for age-related decreases in frontal, central, parietal and occipital electrodes, but not in temporal electrodes. In the aperiodic-adjusted alpha power measures, no significant age effects were observed in any electrode in the canonical alpha band. While the analysis of individual electrodes in the upper aperiodic-adjusted alpha band power only showed significant age-related decreases in three frontal electrodes, the lower aperiodic-adjusted alpha band power showed a very similar, wide spread spatial distribution of age-related decreases as in its total power measure (see Figs. 5A and 6A).

### 3.3.2. Single dataset analysis

Auxiliary analyses were performed to outline the spatial distribution of each age effect in the main and the validation datasets separately, which were included in the Bayesian regression model. For both datasets, cluster-based permutation tests indicated that data were not interchangeable between the age groups in the investigated parameters (total and aperiodic-adjusted alpha power measures, IAF, aperiodic...
intercept and exponent), thus rejecting the global null hypothesis that there is no difference between the age group in all tested electrodes. Only in canonical alpha power, no significant cluster was found in the validation dataset, in line with the single electrode Bayesian regression models. Further conclusions about the extent of the significant clusters are not permitted in cluster-based permutation tests (Maris & Oostenveld, 2007; Sassenhagen & Draschkow, 2019). However, Cohen’s d values in rows C and B of Figs. 5–7 indicate that the two datasets generally show similar age-related decreases within each investigated variable.

### 3.4. Source-level analysis

Fig. 8 depicts source reconstructed spatial distributions of the aperiodic-adjusted canonical alpha power measure and the aperiodic exponent. The purpose of this analysis was to descriptively illustrate the spatial distributions observed in the full scalp analysis on the level of brain sources, no additional statistical tests were performed here. Similar to the topographical results (see Fig. 6), there was a wide spread age-related decrease of the aperiodic exponent across the cortex. For the aperiodic-adjusted canonical alpha power, age-related

|                          | ICC  | Proportion in limits of agreement |
|--------------------------|------|----------------------------------|
|                           | young | old | young | old |
| Total canonical alpha power | .87  | .82 | .95  | .95 |
| Aperiodic-adjusted canonical alpha power | .87  | .86 | .94  | .95 |
| Total lower alpha power | .88  | .84 | .94  | .96 |
| Aperiodic-adjusted lower alpha power | .87  | .86 | .95  | .96 |
| Total upper alpha power | .88  | .85 | .94  | .96 |
| Aperiodic-adjusted upper alpha power | .87  | .88 | .94  | .96 |
| Aperiodic intercept | .76  | .77 | .94  | .93 |
| Aperiodic exponent | .79  | .83 | .97  | .92 |
| IAF | .76  | .77 | .93  | .93 |

Table 5 – ICC values and percentage of observations within the limits of agreement in the Bland–Altman plot.

Fig. 8 – Source reconstructed spatial distribution of aperiodic-adjusted alpha power and the aperiodic exponent parameter and age differences in the main dataset (A) and the validation dataset (B). Cohen’s d of the age differences are visualized, cold colors indicate age related decreases. Above each difference plot, the spatial distribution of each corresponding parameter is visualized for each age group.
decreases are observed in frontal, parietal and occipital cortical regions, while temporal regions tend to indicate age-related increases.

For visualizations of the source reconstructed spatial distribution in lower and upper aperiodic-adjusted alpha power, see supplementary figure A.2 in Appendix A.

3.5. Test-retest reliability

Table 5 summarizes the ICC values of each parieto-occipital periodic and aperiodic EEG parameter for both age groups. Data was obtained from the main dataset, in which each participant was measured twice one week apart. Good to excellent reliability was observed for all investigated measures.

Moreover, the proportion of samples within the limits of agreement (± 1.96 sd of the mean difference) of the Bland–Altman plots is reported in Table 5. Fig. 9 depicts the Bland–Altman plot for each EEG parameter. These plots indicate no bias of increased differences between the test and the retest session for higher average values and suggest similar reliabilities for both age groups. For all variables, a high proportion of observations (≥ 92%) was within the predefined limits of agreement (see also Table 5).

3.5.1. Equivalence test
To estimate equivalence of the reliability between the two age groups, bootstrapped ICC values were calculated within each age group for each parameter. For all EEG parameters, the 90% confidence intervals of the bootstrapped age differences for ICC values were not fully within the predefined equivalence bounds (± 1), indicating that the reliabilities are not equivalent between the two age groups. Fig. 10 visualizes the distribution of age differences in the ICC of each periodic and aperiodic EEG parameter.

3.6. Relation to cognitive scores

No significant associations were found between the cognitive scores and the aperiodic exponent and total and aperiodic-adjusted upper alpha power in the main dataset. Table 6 summarizes the obtained results (see supplementary Figure A.3 in Appendix A for a visualization of the associations between the cognitive scores and the EEG measures in each age group).

Because no significant associations between any measure of alpha power and cognitive scores were found, no further tests were applied to investigate whether the correlations between aperiodic-adjusted alpha power and cognitive scores is larger as compared to total alpha power and cognitive scores (as described in hypothesis H5b).

Finally, equivalence tests were applied to investigate whether there was no relation between the cognitive scores and the measures of alpha power and the aperiodic exponent. Using the equivalence bounds of $r = ±1$, no significant result (i.e. equivalence) was found (see A.3 in Appendix A). Consequently, although no significant correlations were found, based on the here applied tests it cannot be concluded that there are no effects between alpha power and the aperiodic exponent and the cognitive scores.

4. Exploratory analysis

4.1. Control analysis on possible bias of gender

To exclude the possible bias of the unbalanced distribution of gender in the different age groups, additional control analyses were implemented. In these analyses, the control variable gender was added when fitting the Bayesian model to data of the parieto-occipital electrode cluster:

$$ [\text{dv's}] \sim \text{age}_{\text{group}} + \text{gender} + (1 | \text{participantID}) $$

As described in 2.6.2, these models were fit to the same pairs of dependent variables, and were separately fit to the main and the validation dataset, passing the posterior distribution obtained from the main dataset as priors to the validation analysis. Thus, information was combined across the datasets. Results were highly consistent with those observed from the preregistered analysis reported in Table 3 (see supplementary table A.2 in Appendix A).

4.2. Relation to cognitive scores

The preregistered analysis investigated the relation of periodic and aperiodic activity with cognitive scores separately for each age group of the main dataset. Additional exploratory analyses were implemented which combined T1 data the two age groups. Therefore six linear models were estimated, each predicting one of the three EEG measures by one of the two cognitive score while controlling for age:

$$ \text{EEG parameter} \sim \text{cognitive score} + \text{age}_{\text{group}} $$

Results are displayed in Table 7. In contrast to the preregistered analysis, here a significant relation with the TMT B/A score was found for the aperiodic-adjusted upper alpha power measure when controlling for age. The estimate for the relation between TMT B/A and total upper alpha power was highly similar, yet just failed to reach significance. Supplementary exploratory analysis further indicated no significant results in the lower alpha band (see supplementary table A.4 in Appendix A).

4.3. Correlations among the different measures of periodic and aperiodic EEG activity

Exploratory correlational analyses of the main dataset revealed that total measures of alpha power generally show higher correlations with the aperiodic signal components as compared to aperiodic-adjusted alpha power (see Table 8). The aperiodic intercept showed stronger correlations with total alpha power measures than the aperiodic exponent. Furthermore, lower and upper aperiodic-adjusted alpha power were highly correlated ($r = .94$).
5. Discussion

First, outcome-neutral tests and quality checks assured that the obtained data and results are of adequate quality to test the stated hypothesis. The well-replicated finding of age-related decreases in total alpha power (as well as age-related decreases of the IAF) was observed across all independent datasets. Additionally, both the conventional and the aperiodic-adjusted alpha power measures showed the expected, typically observed spatial distribution, with highest power over parietal and occipital electrodes. Furthermore, the objective quality assessment of the preprocessing pipeline excluded datasets of

![Fig. 9](image_url)

**Fig. 9** — Bland–Altman plots visualizing test-retest reliability for the different measures of alpha power, the aperiodic intercept and exponent and the individual alpha frequency in the main dataset. *X*-axes indicate the mean value of the two assessments of each sample, *y*-axes the difference between the two recording sessions. Dashed lines represent limits of agreement, defined as the mean difference between the two measurements ±1.96 standard deviations.

![Fig. 10](image_url)

**Fig. 10** — Distribution of bootstrapped age differences in the ICC for each investigated EEG parameter. Red markers indicate the 90% confidence intervals of the bootstrapped age differences, which are used to determine equivalence (i.e. confidence interval fully within equivalence bounds).

| Table 6 — Spearman correlations between the resting state EEG measures (total and aperiodic-adjusted upper alpha power, aperiodic exponent) and cognitive scores (TMT B/A score, digit span backwards score). |
|---|---|
| | TMT B/A: *r* (P) | Digit span backwards: *r* (P) |
| | young | old | young | old |
| Total upper alpha power | .12 (.25) | .12 (.25) | .04 (.67) | −.06 (.55) |
| Aperiodic-adjusted upper alpha power | .18 (.08) | .08 (.43) | .01 (.90) | −.10 (.34) |
| Aperiodic exponent | .02 (.83) | .10 (.35) | .10 (.31) | −.03 (.75) |

5. Discussion

First, outcome-neutral tests and quality checks assured that the obtained data and results are of adequate quality to test the stated hypothesis. The well-replicated finding of age-related decreases in total alpha power (as well as age-related decreases of the IAF) was observed across all independent datasets. Additionally, both the conventional and the aperiodic-adjusted alpha power measures showed the expected, typically observed spatial distribution, with highest power over parietal and occipital electrodes. Furthermore, the objective quality assessment of the preprocessing pipeline excluded datasets of
Table 7 – Results of the 6 linear models, each predicting one of the EEG measures by one of the two cognitive scores while controlling for age.

| Outcome                          | TMT B/A                                | Digit span backwards |
|----------------------------------|----------------------------------------|----------------------|
|                                  | beta_\text{age} (P)                    | beta_\text{score} (P)|
| Total upper alpha power          | -.25 (.005)                            | -.25 (.007)          |
| Aperiodic-adjusted upper alpha power | -.18 (.007)                           | -.19 (.008)          |
| Aperiodic exponent               | -.23 (<.001)                           | -.23 (<.001)         |

Table 8 – Correlation coefficients between aperiodic signal components and the different measures of alpha band power.

| Canonical alpha band power       | Lower alpha band power                 | Upper alpha band power |
|----------------------------------|----------------------------------------|------------------------|
|                                  | total                                   | Aperiodic -adjusted    | total                   | Aperiodic -adjusted |
| Aperiodic intercept              | .65                                     | .44                    | .68                    | .47                  |
| Aperiodic exponent               | .37                                     | .30                    | .44                    | .36                  |

Note: P values of all reported correlations <.01e-06.

insufficient data quality (8 out of 404 in the main dataset, 2 out of 215 in the validation dataset). When applying standard artifact detection thresholds on the remaining datasets (any data point exceeds the threshold of ±90 μV in the 2 s segments), high data quality was observed: 97.7% of segments were artifact free in the main dataset, and 98.7% in the validation dataset.

With regards to the stated hypothesis, first Hypothesis H1a was confirmed: The old group showed a slower IAF as compared to the young group across datasets. Total power measures of the canonical, the lower and the upper alpha band showed significant age-related decreases, thus confirming also Hypothesis H1b. The hypotheses concerning differential age effects in aperiodic-adjusted alpha power compared to total alpha power were partly confirmed. While there was strong evidence that the aperiodic-adjusted canonical and the upper alpha band power exhibited less age differences than total power measures (confirming hypothesis H2a), no differential age effects were found in the lower alpha band. Therefore, Hypothesis H2b, stating that the lower alpha band exhibits greater age differences in aperiodic-adjusted power than in total power was discarded. With respect to age-related changes in the aperiodic signal component, an age-related decrease of the aperiodic intercept was found as hypothesized in H3a as well as an age-related flattening of the aperiodic signal, confirming Hypothesis H3b.

All total and aperiodic-adjusted power measures as well as the aperiodic intercept and slope showed good to excellent test-retest reliability, thus, Hypothesis H4a was confirmed. However, old and young subjects did not show equivalent levels of test-retest reliability according to the here performed equivalence test, discarding Hypothesis H4b. The preregistered analysis did not show any significant relation between the upper alpha power (H5a) or the aperiodic exponent (H5c) and the working memory scores within each age group. Therefore, H5a and H5c were not confirmed. Testing whether the relationship between aperiodic-adjusted alpha power and cognitive scores is weaker as in total alpha power (H5b) was not applicable, as both measures did not show any significant relation to the scores. However, exploratory analysis combining data of both age groups, while controlling for the effects of age, found similar positive associations between the TMT B/A working memory score with aperiodic adjusted alpha power (\(\beta = .26, P = .037\)) and total alpha power, which just failed to reach significance level (\(\beta = .19, P = .051\)).

Taken together, the present study provided evidence for a reliable age-related decrease in true oscillatory alpha power, while controlling for changes in the IAF and the aperiodic signal, which both showed significant alterations between the young and old groups. The relation of these periodic and aperiodic signal components to age-related cognitive decline demands further investigations.

5.1. Methodological implications

5.1.1. Usage of canonically defined alpha bands

The present study replicated the age-related slowing of the IAF, providing robust results across large datasets. Consequently, canonical alpha bands (e.g. 8–13 Hz) should neither be applied nor interpreted when investigating age-related changes in alpha power. Recent simulation studies further confirmed that a change in the IAF can bias findings in power when using fixed frequency bands (Donoghue, Schaworonkow, & Voytek, 2022). In the context of brain maturation, we previously showed that an increased IAF leads to an underestimation of maturational increases of alpha power (Tröndle et al., 2022). The here preregistered analysis pipeline does not allow direct comparison between canonical and individualized (i.e., IAF based) alpha power, as the latter was divided into a lower and an upper sub band. Yet, consistent with simulations and the previous findings, here the slowing IAF seems to lead to an underestimation of the age-related decline in canonically defined alpha power. Especially in the lower individualized alpha band, there was strong evidence that the age effect in the individualized band power was stronger compared to the canonically defined band (BF = 15.10). This is also reflected in the full scalp Bayesian analyses, where canonical alpha power shows no significant age-related changes, whereas the individualized alpha bands show significant estimates in individual electrodes and generally larger (i.e., more negative) beta estimates across the full scalp (see Figs. 5 and 6).
5.1.2. Relevance of separating periodic and aperiodic signal components in the analysis of alpha power

Importantly, our results support the necessity of separating neural power spectra into periodic and aperiodic components. First, the age-related flattening of the aperiodic signal as well as the decrease of the aperiodic intercept were replicated, showing robust effects not only in the predefined parieto-occipital electrode cluster, but across the full scalp. These alterations of the aperiodic signal induced a bias when investigating age trajectories of alpha power. Bayes factor analysis of data of the parieto-occipital electrode cluster provided strong evidence that age effects in aperiodic-adjusted upper alpha power are smaller as compared to total upper alpha power. Furthermore, post-hoc analyses indicated high correlations between total alpha power measures and the aperiodic intercept, which were less pronounced in aperiodic-adjusted power. Consequently, there is a bias of the aperiodic signal, which leads to an overestimation of age effects in total alpha power, especially in the individualized upper (and the canonical) alpha band. Relatedly, when testing each electrode across the scalp separately, age effects failed to reach significance in parietal and occipital electrodes in the case of upper (and canonical) alpha power in the combined Bayesian models, although the betas (and Cohens d’s in the single datasets) indicate consistent decreases in power in the old subgroup across the scalp (see Fig. 6). This may likely be due to weaker signal to noise ratios on single electrodes compared to the analyses of averaged parieto-occipital electrode cluster values, which indicated significant age-related decreases. Evidence in other recent studies is also mixed for aperiodic-adjusted alpha power: While one recent study found no differences between 85 young and 92 old subjects in alpha peak power (Merkin et al., 2021), a larger scaled study (N = 280) did find age-related power decreases in a canonical alpha band (Thuwal et al., 2021).

Taken together, the present study indicates that although there is a bias of the aperiodic signal overestimating age effects in total alpha power measures, there are age-related decreases also in true oscillatory power (i.e. aperiodic adjusted alpha power). However, it is highlighted that large samples and robust statistical analyses are needed to provide sufficient statistical power for the identification of these latter age effects.

5.2. Differentiation between lower and upper alpha bands

Our analysis indicated that individualized aperiodic-adjusted alpha power shows age-related decreases in both sub bands (upper and lower) in parieto-occipital electrodes. This is in contrast to Polich (1997) who only found age related changes in canonical upper, but not in the lower total parietal alpha power. Furthermore, it was hypothesized that the slowing of the IAF differentially affects the lower and the upper subbands, producing false positive age-related decreases in upper alpha power (Scally et al., 2018) and non-significant findings—or even false positive age-related increases—in the lower alpha band (Klimesch, 1999). Here we conclude that after taking changes in the aperiodic signal and the slowing of the IAF into account, aging is associated with decreased power in both alpha sub bands. Moreover, post hoc correlational analyses indicated that aperiodic-adjusted power in both bands is highly related (r = .94) in the parieto-occipital electrode cluster. Therefore, differentiation between these sub bands is not prerequisite to detect age related changes in resting state alpha power. However, age effects in the lower band tend to be larger as compared to the upper band. Furthermore, these bands have functionally been associated with distinct cognitive domains. While lower alpha power was linked to attentional demands, upper alpha power was linked to working memory processing (e.g., Klimesch et al., 1998; Polich, 1997). The latter is further supported by exploratory analyses in this study, showing significant associations between upper aperiodic-adjusted alpha power and the TMT B/A score when investigating the full main sample, which was not found in lower aperiodic-adjusted alpha power. Consequently, while both sub bands show age-related decreases, the differentiation between the lower and upper alpha band is still relevant from a functional perspective, as they may be associated with different decreases in cognitive functions.

5.2.1. Reliability of classical and newly emerging measures of oscillatory power and aperiodic activity

The present study provided evidence that not only total measures of alpha power, but also aperiodic-adjusted power as well the aperiodic components are reliable markers of the adult and the aging brain. All investigated parameters showed good to excellent test-retest reliability in terms of ICC values. Bland–Altman plots further showed no bias towards a decrease in reliability for smaller or higher values within each EEG parameter. The criterion that 95% of observed difference values should lie within the mean ± 1.96 standard deviations was largely fulfilled for the investigated EEG parameters, with the lowest observed proportion being 92% for the aperiodic exponent.

While one study reported poor reliability of the aperiodic exponent in healthy children (Levin et al., 2020), our results in the young adult sample are in line with previous findings of high reliability in populations of adolescents and young adults (Karahtules et al., 2022; Pathania, Schreiber, et al., 2021; Zsido et al., 2022). As emphasized by Matheson (2019), reliabilities are specific to the investigated study populations and cannot be generalized to other groups, thus we further extended previous findings by providing evidence that old adults show similar high reliability. Also in the aperiodic-adjusted measure of alpha oscillatory power, our findings on young adults are in line with two previous studies on adult females (Zsido et al., 2022) and healthy and autistic children (Levin et al., 2020), reporting high ICC values. As for the aperiodic exponent, the group of old adults also showed high reliabilities. Thus, it is supported that, beyond the established measures of individual alpha frequency and total alpha power, both the aperiodic signal components and aperiodic-adjusted alpha power qualify as potential biomarkers for the aging brain because they fulfill the prerequisite of high reliability.

The here performed statistical tests indicated that old adults do not show equivalent reliabilities as compared to young adults. However, it has to be noted that there are some limitations in this analysis. First, the bootstrapped differences are just an estimate of the true distribution of age differences.
in the ICC. The actual observed differences in the full sample are very small and vary between ICC of .01 and .05 across the investigated parameters. Second, the definition of equivalence bounds (± 1) was an arbitrary decision, which was based on the definition of Cohen (1988) on negligible effect sizes. Similar reasonable cut offs (e.g. ICC difference <.2, based on the criterion that Cohens’ d of .2 is considered a small effect) would have yielded different conclusions. Taken together, although the here preregistered equivalence tests did not show equivalent reliabilities between young and old subjects, both groups indicate very good reliabilities of highly similar magnitude.

A few further limitations are noteworthy in this study, particularly in the here performed Bayesian statistical analyses on the individual electrodes. First, significance levels in these analyses are corrected for multiple comparisons across the different outcome variables, but not for the number of tested electrodes, as the planned cluster based permutation test was not applicable in this specific analysis combining both datasets (see section 3.1). However, the largely consistent results of the cluster based permutation tests in the individual datasets and the spatial distributions of Cohen’s d values do indicate that the significant age effects of the Bayesian regression models are highly unlikely to be caused by false positive errors. This is further supported by the large number of significant electrodes and their coherent spatial distribution.

Second, when passing posteriors of the regression model of one dataset as priors to the analysis of the next dataset, there were minor mismatches between the locations of each electrode within which these priors were updated. The here chosen approach was to match electrodes based on their label in the 10-10 electrode system (e.g. finding the closest match between electrode “Pz” in the 256 EGI electrode cap of the pilot dataset (Luu & Ferree, 2000), passing its posterior as prior for the electrode with closest match of “Pz” in the 128 EGI electrode cap of the main dataset, and finally to the electrode with the label “Pz” in the ActiCAP of the validation dataset). Because this matching could only be done between a subset of electrodes of the ActiCAP and the 70 electrodes of the main dataset analysis, final topographical results could only be based on 61 electrodes.

5.3. Neurophysiological interpretation

5.3.1. Age-related decrease in alpha power

The Bayesian models combining information across datasets provide robust evidence that, after adjusting for changes in the aperiodic signal and the IAF, aging is associated with decreased power in both the lower and the upper alpha sub-band in the parieto-occipital electrode cluster. This provides new insights into the so far mixed results on age effects in aperiodic-adjusted alpha power (see above, Donoghue, Haller, et al., 2020; Merkin et al., 2021; Thuwal et al., 2021). Topographical plots and source level analysis further indicate that the new measures of aperiodic-adjusted alpha power show the expected spatial distribution in both age groups, being strongest over parietal and occipital regions, where age differences are also observed. Beyond these descriptive confirmatory observations, source level plots may indicate further spatial patterns worth investigating. For example, age differences in aperiodic-adjusted alpha power visualized in Fig. 8 show similarities with the spatial distribution of the default-mode network, which has also been proposed to be related to cortical alpha activity (e.g., Bowman et al., 2017; Jann et al., 2009). Application of network based source parcellations (Yeo et al., 2011) might provide additional insights into the possible role of the default-mode network in age differences of aperiodic-adjusted alpha power, which are however beyond the scope of the present report. Future studies are highly encouraged to further explore the neural generators of aperiodic-adjusted alpha power and its age-related decrease in power.

The present findings on the true oscillatory signal (i.e. aperiodic-adjusted alpha power) do not oppose current neurophysiological interpretations, which were based on possibly confounded findings of age-related decreases in total alpha power (Babiloni et al., 2006; Hoshi & Shigihara, 2020; Ishii et al., 2017; Rossini, Rossi, Babiloni, & Polich, 2007; Wang et al., 2020). In more detail, these interpretations link age-related decline in resting state alpha power to an increased excitability of thalamo-cortical and cortico-cortical interactions (Pfurtscheller & Da Lopes Silva, 1999; Steriade & Llinás, 1988). This increased excitability can be explained by the age-related gradual loss of cholinergic function in the basal forebrain (Sarter & Bruno, 1998; Schliebs & Arendt, 2011). The basal forebrain forms main cholinergic inputs to thalamic nuclei (Sokhadze et al., 2019), which are considered key structures in the generation of cortical alpha oscillations (Lopes da Silva, Fernando H. et al., 1980; Schreckenberger et al., 2004). Animal models further support this theory by showing that experimentally impairing cholinergic forebrain function led to decreases in alpha power (Gallagher & Colombo, 1995; Ricceri et al., 2004), and that stimulation of cholinergic receptors in the reticular thalamic nucleus and thalamo-cortical cells produces alpha oscillatory activity (Vijayan & Kopell, 2012). In humans, this is consistent with observed decreases of alpha power in patients suffering from Alzheimer dementia and mild cognitive impairment, which are conditions that are characterized by impaired cholinergic forebrain function (Babiloni et al., 2004; Diers, Ihl, Frolich, & Maurer, 1993; Kuskowski, Mortimer, Morley, Malone, & Okaya, 1993; Moretti et al., 2004; Rodriguez, Copello, Vitali, Perego, & Nobili, 1999). Thus, it is hypothesized that the decreased cholinergic input in the thalamus leads to decreases of power in the cortical alpha oscillations during aging. Functionally, Babiloni et al. (2006) hypothesized that these neurobiological changes may be associated with decreased performance in visual-spatial attention and the regulation of attention for memory processes. Correspondingly, performance scores in a visual-spatial working memory task (TMT B/A) were significantly associated with the power of alpha oscillations when using the full sample and controlling for age in the present study. Note that the preregistered analysis investigating this association within each age group separately did not show significant results, possibly due to limited power when splitting the sample into two sub groups or due to limited between subject variability within the age groups.
5.3.2. Age-related changes in the aperiodic signal

An age-related decrease in the aperiodic intercept and exponent was observed in the parieto-occipital electrode cluster and across the full scalp in the topographical analyses as well as in the source level analysis of the aperiodic exponent. These findings are in line with other recent reports investigating age-related changes in the aperiodic signal components (Donoghue, Haller, et al., 2020; Merkin et al., 2021; Thuwal et al., 2022).

The decrease of the aperiodic intercept may indicate decreased neuronal population spiking activity (Donoghue, Haller, et al., 2020; Manning, Jacobs, Fried, & Kahana, 2009) in old adults. However, interpretations of changes in the aperiodic intercept need to be done with caution, as this component is strongly affected by non-neural changes. E.g., it has been shown that the skull conductivity decreases in older adults (Antonakakis et al., 2020) which yields generally lower EEG amplitudes; an effect that can be captured by a decrease of the aperiodic intercept. Furthermore, the mere flattening of the aperiodic signal inevitably yields a decrease in the aperiodic intercept. Without a well-informed estimate at which frequency the aperiodic signal rotates (i.e., flattens), it is not possible to disentangle these highly correlated observations. Future research is needed to gain more precise insights into age-related changes in the aperiodic intercept.

While disentangling age effects in the aperiodic intercept is difficult, decreases in the aperiodic slope can be interpreted in terms of the neural noise hypothesis of aging (Voytek & Knight, 2015). This hypothesis states that age-related cognitive decline is caused by increased occurrence of temporally decorrelated spikes (i.e., noise) which are not involved in encoding of information or network communication. These irregular spikes decouple the synchronization mechanisms between brain regions, which leads to communication errors. This increased occurrence of errors in the communication between brain regions in turn results in age-related cognitive deficits (Voytek & Knight, 2015). The irregular spikes are presumably caused by greater local positive excitatory feedback, driven by an increased excitation-inhibition ratio (Voytek & Knight, 2015). This increased neural excitation-inhibition ratio has been linked to a flattened aperiodic slope both in computational models and animal studies (Gao et al., 2017). In line with this theory are findings that show the decrease of the aperiodic slope to be associated with more asynchronous activity in neural populations (Miller et al., 2009; Usher et al., 1995). Therefore, the present findings on the aperiodic exponent further support the neural noise hypothesis of aging. However, no significant associations were found between the two investigated scores of working memory performance (TMT A/B and digit span backwards task) and the resting-state aperiodic exponent parameter. A previous study (Voytek et al., 2015) provided evidence that the age-related cognitive decline in a visual working memory task is mediated by a flattened aperiodic slope, however, in contrast to the present report, changes in the aperiodic signal were assessed during task performance. Few studies investigated the relationship with the resting-state aperiodic signal and cognitive performance. In healthy adult populations, significant associations of the resting-state aperiodic exponent were found with visuomotor performance (Immink et al., 2021) and processing speed (Duyang, Hildebrandt, Schmitz, & Herrmann, 2020). Only one small scaled pilot study related resting-state aperiodic activity to cognitive performance in the context of aging (Pathania, Clark, et al., 2021a). The authors reported significant mediating effects of the aperiodic exponent in the relation between age and a composite score of a cognitive test battery (The Repeatable Battery for the Assessment of Neuropsychological Status, Randolph, Tierney, Mohr, & Chase, 1998). However, the aperiodic exponent showed no significant associations with performance in any sub task besides the “Coding” sub score. Consequently, more robust measures of cognitive performance than the here investigated scores of single working memory tasks are probably needed to provide further information whether the aperiodic signal is related to cognitive aging.

Notably, while the present report found widespread cortical decreases of the aperiodic exponent, age-related changes in subcortical brain sources might show a different pattern. Using MEG, Hinault, Baillet, & Courtney (2022) recently observed age-related increases of the aperiodic exponent in the hippocampus. Contrary to our findings, this subcortical aperiodic exponent did show a relation to cognitive performance (visual short term memory task). However, the here performed analyses are limited to cortical sources as individual MRI based head models and individual electrode locations are required to provide sufficient precision for the estimation of deep brain sources. Future studies are needed to further investigate possible distinct aging trajectories of the aperiodic exponent in cortical and subcortical brain areas.

5.3.3. Link between age-related changes in alpha power and the aperiodic exponent

The findings of age-related decreases in alpha power and a flattened aperiodic slope are highly compatible. In fact, these two phenomena should not be interpreted in isolation of each other, as they may both reflect properties of the same neurobiological changes. Post hoc performed correlational analysis indicate highly significant correlations of the aperiodic signal components not only with total alpha power, but also with the periodic measure of alpha power after adjusting for changes in the aperiodic signal. This association between the aperiodic slope and aperiodic-adjusted alpha power has also been observed in another recent study (Kosciessa, Grandy, Garrett, & Werkle-Bergner, 2020). From the above described neurobiological point of view, this correlation is very reasonable. In this framework, decreased thalamic inhibitory control over cortical areas (due to impaired cholinergic input) is reflected in decreased cortical alpha power. This decreased inhibitory control (i.e., decreased alpha power) would lead to higher cortical excitability, and therefore increased ratio of excitation over inhibition and higher level of neural noise. As described above, these phenomena are reflected in the decrease of the aperiodic exponent. This is further supported by a combined EEG-fMRI study which indicated that under thalamic
guidance, decreased parietal alpha power allows for increased parietal excitability (e.g. flattened aperiodic signal) in specific task conditions (Kosciessa, Lindenberger, & Garrett, 2021). Consequently, the age-related cognitive decline may speculatively be explained by this combinatorial effects, in which the decreased alpha oscillatory activity allows for more neural noise which in turn disrupts neural communication. Therefore, against our initial hypothesis, in this framework the aperiodic slope does not merely confound findings in the relation between alpha power and cognitive performance, but both EEG parameters may be associated with age-related cognitive decline. Future research is needed to explore this theory in more detail.

6. Conclusions and outlook

The present registered report showed that aging is accompanied by a decreased intercept and exponent of the aperiodic signal. These changes in the aperiodic signal lead to an overestimation of the age-related decreases in alpha power. Therefore, the importance of the separation between periodic and aperiodic signal components is highlighted. Yet, also after accounting for the aperiodic signal, alpha power is significantly reduced in older adults. Furthermore, these newly emerging EEG parameters (aperiodic components and aperiodic-adjusted power measures) show a high test-retest reliability, hence they qualify as markers of the aging brain. From a neurobiological point of view, it may be hypothesized that the decreased alpha oscillatory activity represents age-related changes in the basal forebrain, leading to disrupted thalamic cortical inhibitory control. This may allow for increased neural noise (i.e. flattened aperiodic slope) in the aging brain, which is, according to the neural noise hypothesis of aging, in turn related to a decline in cognitive function. Future research is needed to further explore the relation of the observed neurophysiological changes with the hypothesized neurobiological alterations and clarify the relation of these phenomena to age-related loss of performance in cognitive domains.

6.1. Sample size and data exclusion statement

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

CRediT author statement

Marius Trondle: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Visualization. Tzvetan Popov: Methodology, Formal analysis, Writing - review & editing. Andreas Pedroni: Conceptualization, Methodology, Formal analysis, Writing - review & editing. Christian Pfeiffer: Writing - review & editing. Zofia Baranczuk-Turska: Methodology. Nicolas Langer: Conceptualization, Methodology, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare no competing interests.

Open practices

The study in this article earned Open Data, Open Materials and Preregistered badges for transparent practices. Materials and data for the study are available at https://osf.io/8e2kd/

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Supplementary data

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REFERENCES

Alexander, L. M., Escalera, J., Ai, L., Andreotti, C., Febre, K., Mangone, A., et al. (2017). An open resource for transdiagnostic research in pediatric mental health and learning disorders. Scientific Data, 4(1), Article 170181.

Amthauer, R. (1973). IST 70. Intelligenz-Struktur-Test. Göttingen: Hogrefe.

Antonakakis, M., Schrader, S., Aydin, Ü., Khan, A., Gross, J., Zervakis, M., et al. (2020). Inter-subject variability of skull conductivity and thickness in calibrated realistic head models. Neuroimage, 223, Article 117353.

Babayan, A., Erbey, M., Kumral, D., Reinelt, J. D., Reiter, A. M. F., Robbig, J., et al. (2019). A mind-brain-body dataset of MRI, EEG, cognition, emotion, and peripheral physiology in young and old adults. Scientific Data, 6(1), Article 180308.

Babiloni, C., Barry, R. J., Başar, E., Binowska, K. J., Cicocki, A., Drinkenburg, W. H. I. M., et al. (2020). International Federation of Clinical Neurophysiology (IFCN) - EEG research workgroup: Recommendations on frequency and topographic analysis of resting state EEG rhythms. Part 1: Applications in clinical research studies. Clinical Neurophysiology Official Journal of the International Federation of Clinical Neurophysiology, 131(1), 285–307.

Babiloni, C., Binetti, G., Cassarino, A., Dal Forno, G., Del Percio, C., Ferreri, F., et al. (2006). Sources of cortical rhythms in adults during physiological aging: A multicentric EEG study. Human Brain Mapping, 27(2), 162–172.

Babiloni, C., Binetti, G., Cassetta, E., Cerboneschi, D., Dal Forno, G., Del Percio, C., et al. (2004). Mapping distributed sources of cortical rhythms in mild Alzheimer’s disease. A multicentric EEG study. Neuroimage, 22(1), 57–67.

Baddeley, A. (2000). The episodic buffer: A new component of working memory? Trends in Cognitive Sciences, 4(11), 417–423.

Barret, T. (2019). Bayesian Power Analysis with ‘data.table’, ‘tidyverse’, and ‘brms’. [Blog post]. July 21 https://tysonbarrett.com/jekyll/update/2019/07/21/BayesianSims/.

Baumler, G. (1974). Lern-und gedächtnisfest: LGT-3. Hogrefe.
Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Computational Intelligence and Neuroscience, Article 156869, 2011.

Ouyang, G., Hildebrandt, A., Schmitz, F., & Herrmann, C. S. (2020). Decomposing alpha and 1/f brain activities reveals their differential associations with cognitive processing speed. Neuroimage, 205, Article 116304.

Palva, S., & Palva, J. M. (2007). New vistas for alpha-frequency band oscillations. Trends in neurosciences, 30(4), 150–158.

Pathania, A., Clark, M., Cowan, R., Euler, M., Duff, K., & Lohse, K. R. (2021). Relating resting EEG power spectra to age-related differences in cognitive performance: An. medRxiv.

Pathania, A., Schreiber, M., Miller, M. W., Euler, M. J., & Lohse, K. R. (2021). Exploring the reliability and sensitivity of the EEG power spectrum as a biomarker. International journal of psychophysiology official journal of the International Organization of Psychophysiology, 160, 18–27.

Pedroni, A., Bahreini, A., & Langer, N. (2019). Automatic: Standardized preprocessing of big EEG data. Neuroimage, 200, 460–473.

Pfurtscheller, G., & Da Lopes Silva, F. H. (1999). Event-related EEG/C19 Psychophysiology, 160, 152.

Pion-Tonachini, L., Kreutz-Delgado, K., & ICLabel, M. S. (2019). An automated electroencephalographic independent component classifier, dataset, and website. Neuroimage, 198, 181–197.

Polich, J. (1997). EEG and ERP assessment of normal aging. Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section, 104(3), 244–256.

Posthumus, D., Neale, M. C., Boomsma, D. I., & Geus, EJ de (2001). The EEG spectral profile to stage Alzheimer disease. Progress in Neurobiology, 83, 329–353.

Roubicek, J. (1977). The electroencephalogram in the middle-aged and the elderly. Journal of the American Geriatrics Society, 25(4), 145–152.

Sánchez-Cubillo, I., Periáñez, J. A., Adrover-Roig, D., Rodriguez-Sánchez, J. M., Rios-Lago, M., Tirapu, J. E. E. A., et al. (2009). Construct validity of the trial making test: Role of task-switching, working memory, inhibition/interference control, and visuomotor abilities. Journal of the International Neuropsychological Society, JINS, 15(3), 438–450.

Sarter, M., & Bruno, J. P. (1998). Age-related changes in rodent cortical acetylcholine and cognition: Main effects of age versus age as an intervening variable. Brain Research Reviews, 27(2), 143–156.

Sassenhagen, J., & Draschek, D. (2019). Cluster-based permutation tests of MEG/EEG data do not establish significance of effect latency or location. Psychophysiology, 56(6), Article e13335.

Scally, B., Burke, M. R., Bunce, D., & Delvenne, J.-F. (2018). Resting-state EEG power and connectivity are associated with alpha peak frequency slowing in healthy aging. Neurobiology of Aging, 71, 149–155.

Schliebs, R., & Arendt, T. (2011). The cholinergic system in aging and neuronal degeneration. Behavioural Brain Research, 221(2), 555–563.

Schreckenberger, M., Lange-Asschenfeldt, C., Lange-Asschenfeld, C., Lochmann, M., Mann, K., Siessmeier, T., et al. (2004). The thalamus as the generator and modulator of EEG alpha rhythm: A combined PET/EEG study with lorazepam challenge in humans. Neuroimage, 22(2), 637–644.

Sedgwick, P. (2013). Limits of agreement (Bland-Altman method). Bmj: British Medical Journal, 346, f1630.

Smit, C. M., Wright, M. J., Hansell, N. K., Geffen, G. M., & Martin, N. G. (2006). Genetic variation of individual alpha frequency (IAF) and alpha power in a large adolescent twin sample. International Journal of Psychophysiology, 61(2), 235–243.

Sokhadze, G., Campbell, P. W., & Guido, W. (2019). Postnatal development of cholinergic input to the thalamic reticular nucleus of the mouse. European Journal of Neuroscience, 49(8), 978–989.

Steriade, M., & Llinás, R. R. (1988). The functional states of the thalamus and the associated neuronal interplay. Physiological reviews, 68(3), 649–742.

Thatcher, R. W., North, D., & Biver, C. (2005). EEG and intelligence: Relations between EEG coherence, EEG phase delay and power. Clinical Neurophysiology, 116(9), 2129–2141.

Thuwal, K., Banerjee, A., & Roy, D. (2021). MEG Oscillatory and Aperiodic neural dynamics contribute to different cognitive aspects of short-term memory decline through lifespan.

Tombaugh, T. (2004). Trail Making Test A and B: Normative data stratified by age and education. Archives of Clinical Neuropsychology, 19(2), 203–214.

Trondle, M., Popov, T., Dziemian, S., & Langer, N. (2022). Decomposing the role of alpha oscillations during brain maturation. Elife, 11, Article e77571.

Usher, S., & Olami. (1995). Dynamic pattern formation leads to 1/f noise in neural populations. Physical review letters, 74(3), 306–329.

van Veen, B. D., van Drongelen, W., Yuchtman, M., & Suzuki, A. (1997). Localization of brain electrical activity via linearly constrained minimum variance spatial filtering. IEEE Transactions on Biomedical Engineering, 44(9), 867–880.

Vijayan, S., & Kopell, N. J. (2012). Thalamic model of awake alpha oscillations and implications for stimulus processing. Proceedings of the National Academy of Sciences of the United States of America, 109(45), 18553–18558.

Voytek, B., & Knight, R. T. (2015). Dynamic network communication as a unifying neural basis for cognition, development, aging, and disease. Biological Psychiatry, 77(12), 1089–1097.

Voytek, B., Kramer, M. A., Case, J., Lepage, K. Q., Tempesta, Z. R., Knight, R. T., et al. (2015). Age-related changes in 1/f neural electrophysiological noise. Journal of Neuroscience, 35(38), 13257–13265.

Vysata, O., Kakul, J., Prochazka, A., Pazdera, L., & Valis, M. (2012). Age-related changes in the energy and spectral composition of EEG. Journal of Neurophysiology, 44(1), 63–67.

Wang, C., Kang, M., Li, Z., Li, Y., Guan, M., Zou, Z., et al. (2020). Altered relation of resting-state alpha rhythm with blood oxygen level dependent signal in healthy aging: Evidence by EEG-fMRI fusion analysis. Clinical Neurophysiology Official Journal of the International Federation of Clinical Neurophysiology, 131(9), 2105–2114.
Wechsler, D. (1997). *WAIS-III Administration and scoring manual*. San Antonio, TX: The Psychological Association.

Welch, P. (1967). The use of fast fourier transform for the estimation of power spectra: A method based on time averaging over short, modified periodograms. *IEEE Transactions on Audio and Electroacoustics, 15*(2), 70–73.

Wen, H., & Liu, Z. (2016). Separating fractal and oscillatory components in the power spectrum of neurophysiological signal. *Brain Topography, 29*(1), 13–26.

Winawer, J., Kay, K. N., Foster, B. L., Rauschecker, A. M., Parvizi, J., & Wandell, B. A. (2013). Asynchronous broadband signals are the principal source of the BOLD response in human visual cortex. *Current Biology CB, 23*(13), 1145–1153.

Yeo, B. T. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., et al. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of neurophysiology, 106*(3), 1125–1165.

Zou, G. Y. (2007). Toward using confidence intervals to compare correlations. *Psychological methods, 12*(4), 399–413.

Zsido, R. G., Molloy, E. N., Cesnaite, E., Zheleva, G., Beinhöhl, N., Scharrer, U., et al. (2022). One-week escitalopram intake alters the excitation-inhibition balance in the healthy female brain. *Human Brain Mapping, 43*(6), 1868–1881.