Aperiodic and periodic components of ongoing oscillatory brain dynamics link distinct functional aspects of cognition across adult lifespan

https://doi.org/10.1523/ENEURO.0224-21.2021

Cite as: eNeuro 2021; 10.1523/ENEURO.0224-21.2021
Received: 18 May 2021
Revised: 19 August 2021
Accepted: 31 August 2021

This Early Release article has been peer-reviewed and accepted, but has not been through the composition and copyediting processes. The final version may differ slightly in style or formatting and will contain links to any extended data.

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1. **Title:** Aperiodic and periodic components of ongoing oscillatory brain dynamics link distinct functional aspects of cognition across adult lifespan

2. **Abbreviated Title:** RS brain dynamics linking distinct functional aspects through lifespan

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5. **Author Contributions:** Kusum Thuwal: Design and Conceptualization, formal analysis, Writing - review & editing, Visualization. Arpan Banerjee: Writing - review & editing, Supervision, Funding acquisition. Dipanjan Roy: Design and Conceptualization, Resources, Writing - review & editing, Supervision, Funding acquisition.

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7. **Number of Figures:** 12

8. **Number of Tables:** 3

9. **Number of Multimedia:** NA

10. **Number of words for abstract:** 245

11. **Number of words for Significance Statement:** 112

12. **Number of words for Introduction:** 756

13. **Number of words for Discussion:** 2010

14. **Acknowledgements:** This study was supported by NBRC Core funds and Computing Facility, Ramalingaswami Fellowships (Department of Biotechnology, Government of India) to DR (BT/RLF/Re-entry/07/2014). DR was also supported by SR/CSRI/21/2016 extramural grant from the Department of Science and Technology (DST) Ministry of Science and Technology, Government of India. DR and AB acknowledge the generous support of the NBRC Flagship program BT/ MEDIII/ NBRC/ Flagship/ Program/ 2019: Comparative mapping of common mental disorders (CMD) over lifespan. Data collection and sharing for this project was provided by the Cambridge Centre for Aging and Neuroscience (Cam-CAN). Cam-CAN funding was provided by the UK Biotechnology and Biological Sciences Research Council (grant number BB/H008217/1), together with support from the UK Medical Research Council and University of Cambridge, UK. In accordance with the data usage agreement for CAMCAN dataset, the article has been submitted as open access.

15. **Conflict of Interest:** Authors report no conflict of interest.

16. **Funding Resources:** NBRC core, Department of Biotechnology, Govt. of India (Grant Nos: BT/RLF/Re-entry/07/2014) Department of Science and Technology, Ministry of Science and Technology (Grant No. SR/CSRI/21/2016), NBRC Flagship program BT/ MEDIII/ NBRC/ Flagship/ Program/ 2019.
Aperiodic and periodic components of ongoing oscillatory brain dynamics link distinct functional aspects of working memory processing through adult lifespan

ABSTRACT:

Signal transmission in the brain propagates via distinct oscillatory frequency bands but the aperiodic component - 1/f activity - almost always co-exists which most of the previous studies have not sufficiently taken into consideration. We used a recently proposed parameterisation model that delimits the oscillatory and aperiodic components of neural dynamics on lifespan ageing data collected from human participants using Magnetoencephalography (MEG). Since, healthy ageing underlines an enormous change in local tissue properties, any systematic relationship of 1/f activity would highlight their impact on the self-organized critical functional states. Furthermore, we have used patterns of correlation between aperiodic background and metrics of behaviour, to understand the domain general effects of 1/f activity. We suggest that age-associated global change in 1/f baseline, alters the functional critical states of the brain affecting the global information processing impacting critically all aspects of cognition e.g., metacognitive awareness, speed of retrieval of memory, cognitive load and accuracy of recall through adult lifespan. This alteration in 1/f crucially impacts the oscillatory features peak frequency and band power ratio, which relates to more local processing and selective functional aspects of cognitive processing during the Visual Short Term Memory (VSTM) task. In summary, this study leveraging on big lifespan data for the first time tracks the cross-sectional lifespan associated periodic and aperiodic dynamical changes in the resting state to demonstrate how normative patterns of 1/f activity, peak frequency and band ratio measures provide distinct functional insights about the cognitive decline through adult lifespan.

Significance statement: Ageing is accompanied by the decline in cognitive functions and age itself is a major risk factor for Alzheimer’s Disease and other neurological conditions. Our study provides
Magnetoencephalogram (MEG) 1/f aperiodic and periodic markers across the healthy adult lifespan and shows that different frequency bands and their spectral features (aperiodic and periodic component) mediate age-related changes across different brain regions, in multiple cognitive and metacognitive domains, which not only provides us with a better understanding of the ageing process but would also help in better prevention of cognitive impairments. A clear characterization of the association between baseline oscillatory component, 1/f activity, band ratio, healthy ageing and cognition, is established in this study.

**INTRODUCTION:**

Spontaneous brain dynamics indexed by variation of neuro-electromagnetic potential may reflect the local as well global change associated with healthy ageing processes that guide behavioural response through lifespan (Bishop et al., 2010; Foster et al., 2015; Sahoo et al., 2020). While the periodic component of spontaneous activity has been extensively studied as an objective measure for cognitive phenotyping (Klimesch, 1999; Knyazev, 2007; Schutter & Knyazev, 2012), the non-oscillatory/aperiodic background component also known as “1/f” activity received less attention compared to the former. This spontaneous 1/f aperiodic brain dynamics almost always pervasively co-exists in EEG/MEG/LFP signals (Lyne et al., 1992; Beggs et al., 2003; Linkenkaer-Hansen et al., 2001; Bédard et al., 2006; Voytek et al., 2015) and critically influence oscillatory signatures in the context of healthy ageing and constrain task performance (Voytek et al., 2015; Donoghue et al., 2020). As we age, we are faced with the likelihood that our cognitive faculties will decline for example, ascertain memory (Nyberg et al, 2012), shift of sustained attention (Gazzaley et al., 2005), and processing speed (Salthouse et al., 2010). There were recent attempts to relate 1/f activity - where it is being considered as a marker of “neural noise”- with N900 lexical prediction (Dave et al., 2018), working memory (Voytek et al., 2020) and grammar learning (Cross et al., 2020).

The existence of ubiquitous “1/f” activity in neuronal systems organized across various spatial scales is one of the key features of signal variability and collectively referred to as “noise”. However, a recent
perspective suggests a serious reconceptualization is necessary to define what constitutes the ‘signal of interest’ or ‘noise’ in neuroscience (Uddin et al., 2020). The characteristics of 1/f component - slope and offset - of the ongoing oscillatory power has been found to be dynamic in nature. One possible mechanism for this dynamical change is an increased baseline activity (Voytek et al., 2015) or at a more fundamental level, a phenomenon called self-organized criticality (Bak et al., 1987). In Neuroscience, the presence of critical brain states can shape an organism’s ability to optimally switch between task states (Buzsáki, 2006). However, some studies have postulated that the origin of 1/f may lie in the tissue properties (Bedard et al., 2006). Therefore, we hypothesized that ageing is consonant with alteration of physiological properties in brain tissue, so any changes along ageing dimension in 1/f owes its origin to the tissue properties. Subsequently, we propose that prospective age-corrected correlations between 1/f and behavioural performance in tasks will reveal if the tissue properties can alter the self-organized criticality of functional brain states and subserve as a non-specific mediator of behaviour and cognitive functions.

Other than the characteristics of 1/f component - slope and offset, physiological ageing has been further characterized by progressive change in oscillatory power, central frequency, and functional connectivity (Voytek et al., 2015; Tran et al., 2020; Sahoo et al., 2020; Murty et al., 2020). For example, a consistent line of research associated higher individual peak alpha frequency (PAF) across adulthood with better working memory and better reading comprehension (Angelakis et al., 2004; Clark et al., 2004; Klimesch, 1997). There are also noticeable discrepancies among numerous existing ageing studies based on the estimation of difference of power between younger and elderly individuals in the frequency band of interest (Klass et al., 1995; Aurlien et al., 2004; Cummins et al., 2007; Stomrud et al., 2010; Ishii et al., 2017; Scally et al., 2018, Sahoo et al., 2020). Hence, it is often notoriously difficult to reconcile those age-associated oscillatory findings during spontaneous activity and trusting power changes in the relevant frequency band were estimated accurately. One possible reason for this inconsistency might be the mixing of oscillatory power with the aperiodic background 1/f activity, which was not taken into sufficient consideration by most of the studies.
On the other hand, frequency band ratio is a common measure in investigating attention deficit hyperactivity disorder (ADHD) (Lubar, 1991; Snyder 2006; Arns et al., 2014), executive functioning (Lubar, 1991; Angelidis et al., 2016; Gordon et al., 2018; van Son et al., 2019) and working memory capacity (Moran et al., 2010). We propose here that both shifts in individual peak frequency (PF) and band ratio (BR) index clearly different aspects of functional changes associated with ageing impacting short-term working memory speed and accuracy of retrieval on one hand and cognitive capacity on the other. Taking together, we suggest the three different measures, 1/f slope-offset reflecting aperiodic activity, PF and BR reflecting periodic activity provide distinct functional insights about the neural underpinning of the healthy ageing process.

METHODS

1. Participants:

The Cambridge Centre for Ageing and Neuroscience (Cam-CAN) is a large-scale, multimodal, cross-sectional adult lifespan (18-88) population-based study. The Cam-CAN consists of 2 stages. In stage 1, 2681 participants had gone through general cognitive assessments at their home. Tests for hearing, vision, balance, and speeded response were also assessed. Additionally, measures taken in stage 1 served to screen participants for stage 2. Those with poor hearing, poor vision, with neurological diseases such as stroke, epilepsy, or a score less than 25 in MMSE (cognitive assessment examination) were excluded from the further participation. From stage 1 to stage 2, 700 participants were screened (50 men and 50 women from each age band). All screened participants were recruited for testing at the Medical Research Council (UK) Cognition and Brain Sciences Unit (MRC-CBSU) in Cambridge, UK. In this stage, MRI scans, MEG recordings and cognitive task data were collected, all the participants performed a range of psychological tests and neuroimaging assessments, but only the MEG RS data and VSTM task data are included in this study. Out of 700 participants, Magnetoencephalogram (MEG) data from 650 subjects
were available. Age values of participants were divided into 4 age groups for categorical analysis (See Statistical analysis): Young Adults (YA), Middle Elderly (ME), Middle-Late (ML), Older Adults (OA).

Earlier studies have done similar grouping (Chan et al., 2014; Sahoo et al., 2020). 70 participants were randomly chosen from each age group resulting in a total of N=280 subjects comprising all four important stages of adult lifespan (Table 1.)

2. Data acquisition:

2.1 MEG Resting-State data

MEG Data used for this study were obtained from the Cam-CAN repository (available at http://www.mrc-cbu.cam.ac.uk/datasets/camcan/) (Taylor et al., 2007; Shafto et al., 2014). For all the 700 participants, MEG data were collected by Elekta Neuromag, Helsinki at MRC-CBSU using 306 channels, consisting of 102 magnetometers and 204 orthogonal planar gradiometers. MEG data collection was done in a light magnetically shielded room (MSR). A high pass filter of 0.03 Hz cut off was used to sample the data at 1000Hz. Head-Position Indicator (HPI) coils were used to continuously assess the head position within the MEG helmet. To monitor blinks and eye-movements, two pairs of bipolar electrodes were used to record horizontal and vertical electrooculogram signals. To monitor pulse-related artefacts, one pair of electrodes were used to record electrocardiogram signals. MEG data collected for resting state required the participants to sit still for a minimum of 8mins and 40 sec with their eyes closed. From this subset, 280 participants were included in the present study (70 in each group).

2.2 VSTM Stimuli and Task

In Cam-CAN, the design was adapted from Zhang et al., 2008 (Figure 1). On each trial, participants were presented with 1,2,3, or 4 coloured discs (mimicking different memory load conditions) for 250ms. Following that, a blank screen was presented for 900ms to hold those colours in memory. One of the original locations was highlighted by a thick black border (acting as a probe for participants to remember the colour at that location), and at the same time, a response colour wheel was presented. Participants had
as much time as required to report by touching or clicking, as accurately as possible the remembered hue of the highlighted disc. No feedback was given. After every trial, 830 ms fixation period was there. Participants complete two blocks of 112 trials, with memory load (1, 2, 3 or 4) counterbalanced and randomly intermixed. For each set size (memory load), the following measures (Table 2.) were estimated by fitting the error distribution with a mixture model of von-mises and uniform distributions, proposed by Zhang & Luck (2008) and modified by Bays and Husain (2008). For detailed analysis refer to Zhang et al., 2008; Mitchell et al., (2018). In brief, as a model-free index of performance, the response error—the angular difference between the target color presented and the color reported—was calculated. This model-free index cannot be used to distinguish errors due to imprecise memory of an item, from errors due to reporting the wrong item, or guessing when an item is not kept in memory at all. To estimate these, Maximum likelihood estimation was used to decompose the data from each subject into three parameters that represent a mixture of a uniform distribution of errors and a von Mises distribution of errors. The von Mises distribution is the circular analogue of the gaussian distribution and was used because the tested colour space was circular. The uniform distribution was represented by a single parameter, $P_m$, which is the probability that the probed item was present in memory at the time of the probe. ‘$K$’ is calculated by multiplying the memory load by $P_m$. The von Mises distribution was represented by two parameters, its mean ($\mu$) and its standard deviation (s.d.). $\mu$ reflects any systematic shift of the distribution away from the original colour value. The ‘precision’ of each item held in memory is reported as the reciprocal of the standard deviation of the fitted von-Mises distribution. Subjects indicated their uncertainty in their choice of colour by the length of time they touched the wheel: As they held their finger down, white confidence intervals spread out around the selected point indicating greater uncertainty about their selection. To assess metacognitive awareness, the angular width of the reported confidence intervals provided a trial-by-trial measure of subjective uncertainty. To summarize overall uncertainty for each individual and condition, the mean was taken across trials. Participants with smaller values thus reported more confidence in their responses.
2.3 MEG Data Preprocessing

MEG processed data was provided by Cam-CAN. Preprocessing pipeline included temporal signal space separation, applied on continuous MEG data to remove noise from the HPI coils, environmental sources and continuous head motion correction. For removing the main frequency noise (50 Hz notch filter) and to reconstruct any noisy channel, max filter was used. More details about data acquisition and preprocessing have been presented elsewhere (Shafto et al., 2014; Taylor et al., 2017). Additionally, we performed independent component analysis (ICA) to get rid of the artifacts and removal of higher order harmonics present in different frequency bands in the signal following previous studies (Taylor et al., 2017; Sahoo et al., 2020).

2.4 Data Analysis

We analyzed the MEG and behavioural data in MatLab and python using custom made scripts. We have used Python MNE for preprocessing, standard python libraries including Scipy, Pandas and NumPy for data management and processing, python-matplotlib and seaborn for data visualisation in this study. The analysis pipeline is presented in Figure 2.

2.4.1 Power Spectral Density (PSD) using Welch’s periodogram method

The Power spectrum $S_x(f)$ of a signal $x(t)$ capture how the strength of the signal is distributed in the frequency domain. Using Fast Fourier Transform (FFT), (a variant of Fourier Analysis), the representation of raw signal (time or space) is transformed into a frequency representation of the signal.

Processed MEG data provided in ‘.fif’ format was analysed using Fieldtrip toolbox (Oostenveld et al., 2011). Data for each N=280 subjects were first downsampled from 1000 Hz to 250Hz. The frequency resolution was held at 0.05 Hz. Power spectral density (PSD) was estimated using Welch’s periodogram method (pwelch function) implemented in MATLAB 2019b. For each participant, 102 magnetometer sensor’s time series data resulted in a matrix of size $102 \times T$, where $T$ correspond to the number of time points. Each sensor’s $c$’s time series $x_c(t)$ was further divided into segments of 20s (epochs) without any overlap. Spectrum was estimated for each segment after multiplying the time series segment with a
Hanning window. We estimated a global spectrum, representative of each subject i.e., $S_i(f)$ by taking a grand average of spectrums across all 102 magnetometer channels.

$$S_i(f) = \sum_c s_i(c, f)$$  \hspace{1cm} (1)

For each participant, resulted power spectrum matrix was $v \times c$. For group-wise analysis, each participant’s spectrum was averaged across sensors of interest.

### 2.4.2 Extracting Periodic and Aperiodic Features using a Parameterization model

To separate the periodic (oscillatory) component from the aperiodic component of the signal power spectra we used a recently proposed parameterization model, fitting-oscillations-and-one-over-f (FOOOF toolbox) (for a full description refer to Donoghue et al., 2020). In brief, the PSDs calculated using `pwelch` was given as an input to the FOOOF model, which considers PSDs as a linear sum of aperiodic $1/f$ like characteristics of neural power and it is entirely described by the aperiodic “exponent” and “offset”.

Periodic components describe putative oscillations that describe power above aperiodic component (so-called ‘peaks’, simulated as Gaussian function; are described by Peak Frequency in hertz (Hz); peak power over and above the $1/f$ signal in arbitrary units (au) and bandwidth (Hz). Larger bandwidth in given frequency band indicates the deviation of power from the baseline and the spread across a wider frequency range. This global spread in power across frequency band further quantifies the strength of a signal at a specific frequency and allows for information transfer across wider frequency range. The simulation, for a power spectrum $P$ is described as follows,

$$P = L + \sum_{n=0}^{N} G_n$$  \hspace{1cm} (2)

Where $P$ is the linear sum of the aperiodic signal ‘$L$’ and N Gaussian peaks ‘$Gn$’. For each peak, Gaussian function ‘$G_n$’ is fitted which is modelled as:
\[ G_n = a \cdot e^{-\frac{(F-c)^2}{2w^2}} \]  

(3)

Where ‘a’ denotes the amplitude, ‘c’ denotes the central frequency, ‘w’ denotes the bandwidth of the Gaussian. ‘F’ is the frequency vector. Subsequently, all fitted Gaussians were subtracted from the original power spectrum to get a peak-removed power spectrum (PRPS). Finally, a 1/f signal is estimated from this PRPS using Eq. (4), representing the actual cortical noise. Exponential function in semilog-power space (logged power values and linear frequencies) is used to model the aperiodic signal (initial and final fit both), ‘L’, as:

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

(4)

Where ‘b’ denotes the broadband offset, ‘\( \chi \)’ is the slope, and ‘k’ is the knee parameter, which depends on the bend in the aperiodic signal. ‘F’ is the frequency vector. The FOOOF model described in equation 2 fits the power of a given sensor signal by estimating a linear function ‘L’ for the aperiodic component of the signal and each oscillatory contribution ‘Gn’ is modelled as Gaussian peaks. Moreover, estimated power was fitted across the entire frequency range of 1 to 45 Hz by as no knee was expected in the MEG recordings across 1-50 Hz frequency range (Miller et al., 2009). The number of oscillatory components is determined from the data, with the option to set a maximum number of components as a parameter. The general model assumption here is that oscillatory and aperiodic processes are distinct and separable.

Algorithm was implemented using custom python scripts on the python3 version.

The model was fitted for individual subject and output parameters were averaged across subjects for each group (Figure 3(A)). The settings for the algorithm were set as: (1) peak_width_limits = [0.5, 12]; (2) min_peak_height = 0; (3) max_n_peaks = 12; (4) peak_threshold = 2; (5) aperiodic_mode = “fixed”; and (6) verbos = ‘True’. Oscillations were post-hoc grouped into theta (θ, 4-8 Hz), alpha (8-12 Hz), and Beta (β, 13-30 Hz). For estimating the topographical dynamical changes, the brain was segmented into 5 non-overlapping regions: frontal (number of sensors = 26), parietal (number of sensors = 26), occipital (number of sensors = 24), right and left temporal (number of sensors = 26).
2.5.3 Band Ratio Measures

Additionally, we estimated the band ratios which reflect the quantitative measure of oscillatory activity and are investigated in different cognitive processes; however, they also get impacted by the 1/f background noise (Donoghue et al., 2020). After removing the aperiodic signal using a parametrization method proposed by the Fooof toolbox, periodic values were estimated. Thus, after implementing appropriate parametrization of the aperiodic component of the signal power spectra band ratio values were re-estimated to indicate the true power changes and finally, were grouped into different frequency bands of interest. For each participant, we calculated the ratio of periodic components of different frequencies and averaged across participants for age bin-wise distribution. Band ratio of all the periodic components for each frequency band was then calculated by dividing the average of low band periodic features by the average of high band periodic features. We calculated frequency-specific band ratios of all periodic features.

\[
\text{Band Ratio } (X) = \frac{\text{Avg}(X_{\text{Low Band}})}{\text{Avg}(X_{\text{High Band}})}
\]

(5)

where \( X = PW, CF, BW \)

2.5.4 Statistical Analysis:

We performed both categorical as well as continuous analysis to capture different aspects of age-associated functional differences. For the continuous analysis, we divided the total number of participants into bins of 5 years starting from 18 years, a total of 14 bins and the centre value was taken to be the representative age for each bin. For the categorical analysis, we divided data into the following age stratifications (18-35 years, 36-50 years, 51-64 years, 66-88 years) to get insights about different important stages of adult lifespan and comparison with previous works (Chan et al., 2014; Sahoo et al., 2020). To clearly delineate the effects of periodic and aperiodic features on VSTM features it was necessary to illustrate the effect in different load conditions. Only set size 2 and set size 4 is reported in the main manuscript where we have categorised the set sizes in two load conditions: set size 2 as a low
load condition and set size 4 as a high load condition. We have provided the findings for behavioural features of other set sizes as Extended Data.

**Correlation Analysis:**
Depending on the data distribution, Pearson or Spearman’s correlation was used to estimate the strength between two variables. Estimated functional changes (Peak frequency, aperiodic, and band-ratio measures) and VSTM task measures were correlated with age. Finally, VSTM task measures were correlated with the functional changes that occurs with ageing to elucidate the role of these functional measures in determining behavioural responses.

**Regression Analysis:**
Linear and Non-linear Regression were performed separately considering each Power, central frequency, Bandwidth, slope, offset and band-ratios of periodic features, as the estimated measures (R) of functional changes and Precision, Reaction Time (RT), Metacognitive awareness (d) and memory capacity (k), as the estimated measures (R) of the VSTM behavioural task, while keeping age as an explanatory variable.

\[ R = \beta_0 + \beta_1 \times (\text{age}) \]  
\[ R = \beta_0 + \beta_1 \times (\text{age}) \times \beta_2 \times (\text{age}^2) \]

Linear regression was performed using *fitlm* matlab function. To capture the potential non-linear effects of age, we also added 2\textsuperscript{nd} order polynomial terms to the model, such as:

Linear regression was also performed considering each VSTM task measure as response variable (R) and the functional measure as the explanatory variable (E). (Detailed report is provided in supplementary)

\[ R = \beta_0 + \beta_1 \times (E) \]
All regression tables are provided in the supplementary document. For estimating the significance, first normality of the data distribution was assessed using the Kolmogorov Smirnov test. Based on the data distribution, parametric (t-test) or nonparametric (Wilcoxon rank-sum test) was performed.

**Code Accessibility**

The codes for all the analysis carried out in this paper is freely available to download from https://drive.google.com/drive/folders/1__74tFI1_VnHaV-kj46VAGMGii04T2t?usp=sharing

**RESULTS:**

Using the FOOOF model, we fitted the PSD and from the parametrization model fit, all the simulated Gaussian peaks were removed to analyse the background signal. Thereafter, the aperiodic component of the signal was fitted in the log-log space line ([Extended fig. 3-2](#)) from which 1/f Slope and offset were extracted for each participant. Periodic features - Central Frequency (CF), Power (PW), Bandwidth (BW) - were estimated using peak parameters from the fitted model (refer to the materials and methods section).

To check if the parameterisation using the simulated Fooof model is able to capture lifespan associated changes, we first simulated the model for young and old adults. The model well captured the well-established lifespan associated with slowing down of Peak alpha frequency (PAF) ([Figure 3](#)). Original spectrum, aperiodic fit and full model are being depicted in [Figure 3(B)(C)](##) for YA and OA group respectively (Extended analysis are shown in Extended Data Figures 3-1, 3-2, 3-3, 3-4, 3-5 for model’s output parameters of ME and ML groups). To capture the dynamical changes in the dominant oscillations (highest power peak across all frequencies) across the adult lifespan, the central frequency, power, and bandwidth of the dominant oscillations were also extracted for young and old adults.

**1. Topographical distribution of Aperiodic 1/f component of the signal with Age**

**Increase in Aperiodic 1/f slope and decrease in 1/f intercept**

Aperiodic 1/f slope increases significantly when age was treated as a pseudo-continuous variable ($\beta_1 = +0.0034901$, $R^2 = 0.584$, $p = 0.003$) whereas 1/f offset does not show significant decrease across the
adult lifespan ($\beta_1 = -0.0033423$, $R^2 = 0.3$, $p = 0.03$) (Figure 4(A), (B)). Categorical analysis also confirmed significant difference in the 1/f slope between the OA vs YA ($t$ (140) = 4.38, $p < 0.0001$), ML vs YA ($t$ (140) = 4.07, $p = 0.02$), ME vs YA ($t$ (140) = 2.7749, $p = 0.007$), ME vs OA ($t$ (140) = -2.4581, $p = 0.02$). Categorical difference in 1/f offset was also found between OA vs YA ($t$ (140) = 2.0345, $p = 0.0457$) and ML vs YA ($t$ (140) = -2.3441, $p = 0.02$) (Figure 4(A), 4(B)). Aperiodic fit and full model are being depicted in Figure 3 for YA and OA group respectively, and within group analysis revealed more variability in aperiodic features in the older adults (Slope: SEM = 0.023; Offset: SEM = 0.0404) compared to young adults (Slope: SEM = 0.014; Offset: SEM = 0.0364) (Extended Data Figures 3-3, 3-4). Figure 4C and Figure 4D shows variability in spatial topographies of aperiodic 1/f slope and offset for Young and Old.

2. Topographical distribution of Peak frequency with age

Age-associated slowing of Central Alpha frequency and Beta frequency

For each participant, PF was quantified by estimating the peak power value within the 8-12 Hz and 13-30 Hz for alpha and beta range, respectively. Each participant’s PF was then averaged to get the group-wise estimation of Central Alpha Frequency (CAF). Visual inspection revealed bin 65 to be the outlier (for CAF). After removing the outlier, significant linear age-related decline was found ($\beta_1 = -0.010234$, $R^2 = 0.4$, $p = 0.02$) however, central beta frequency (CBF) showed non-linear decrease with age ($\beta_1 = -0.024068$, $R^2 = 0.462$, $p = 0.007$) (Figure 5(A)). Categorical analysis also revealed significant CAF differences between YA vs OA ($t$ (140) = 4.7551 $p = 0.00001$), YA vs ME ($t$ (140) = 3.4198, $p = 0.001$) and YA vs ML ($t$ (140) = 4.8826, $p = 0.000001$), and for CBF between YA vs OA ($t$ (140) = 1.912, $p = 0.03$). Almost all sensors were found to be contributing to the decrease in CAF in OA whereas the decrease in CBF was mainly contributed by the central sensors (Figure 5(B)). No significant difference was found in the frequencies of dominant oscillation; however, the power of the respective dominant frequencies was found to be significantly different between YA and OA (Extended analysis are shown in Extended Data Figure 5-1).
Age-associated Functional Power change in Alpha, Theta and Beta frequency

We found a robust decline of Alpha power with age ($\beta_1 = -0.0059263$, $R^2 = 0.75$, $p = 0.00005$) (Figure 6(A)). Visual inspection suggests that sensor level Alpha power difference was mainly contributed by the occipital, parietal and left temporal sensors (Figure 6(B)). Significant difference was found between OA vs YA ($t (140) = -3.038$, $p = 0.003$), OA vs ME ($t (140) = -2.2008$, $p = 0.03$) and OA vs ML ($t (140) = -2.2252$, $p = 0.029$). Older adults showed higher Theta power ($M = 0.56 \pm 0.04$) than younger adults ($M = 0.32 \pm 0.02$) ($t (140) = 2.4733$, $p = 0.023$). Significant age effect was also observed with increase in theta power ($\beta_1 = 0.0050947$, $R^2 = 0.363$, $p = 0.022$) (Figure 6(A)), which was mainly contributed by the temporal sensors. In addition, ageing was also associated with an increase in Beta Power ($\beta_1 = 0.002496$, $R^2 = 0.70$, $p = 0.0001$) (Figure 6(A)). Spatial topographies showed Central and frontal sensors to be contributing to this age-related increase in global beta power (Figure 6(B)). Categorical analysis revealed significant differences in Beta power between the YA vs OA ($t (140) = -4.3693$, $p = 0.00004$), YA vs ME ($t (140) = -3.0103$, $p < 0.003$), and YA vs ML ($t (140) = -4.4158$, $p = 0.00003$). Extended analysis is shown in Extended Data Fig. 6-1 displaying the sensor-wise distribution of frequency specific power as a function of age.

Increase in Beta bandwidth with age

Bandwidth reflects the spread of power in the respective frequency range, which for the Beta band was found to be increased across the adult lifespan ($\beta_1 = 0.040345$, $R^2 = 0.58$, $p = 0.001$) (Figure 7(A)). Significant group-wise difference was also seen between YA vs OA ($t (140) = -3.1586$, $p = 0.0024$), YA vs ME ($t (140) = -1.9843$, $p = 0.049$). Increase in beta bandwidth indicates that the beta power tends to be more distributed within the frequency band as we age. This increase was mainly observed over left temporal and central sensors (Figure 7(B)). Bandwidth for Alpha and Theta frequency band did not differ across age groups (Extended Data Figure 7-1). For sensor topography refer to Extended Data Figure 7-2.
3. Topographical distribution of Band-Ratios with age

Band ratio measures have been argued to be a marker of various cognitive measures in healthy adults as well as in pathological conditions (Trammell et al., 2017; Kamiński et al., 2011; Schutter et al., 2005) which also gets affected by 1/f activity. We investigated how these global band ratios change with age after effectively removing the background 1/f activity. We looked at Theta/Alpha (θ/α), Theta/Beta (θ/β) and Alpha/Beta (α/β) band ratios, where the ratio of all periodic features (PW, CF, BW) were analyzed for each frequency band. For all band ratio measures, we calculated correlations between the spectral features of each oscillation-band and age. Here we showed the global change (averaged across all sensors) in the band ratio measures across the lifespan.

The age-associated nonlinear change was mostly observed in frontal and parietal sensors (Figure 8(A)). For age categories, we found a significant difference between OA vs ME (t (134) = 2.38, p = 0.018), OA vs ML (t (134) = 3.19, p = 0.0018), YA vs ME (t (138) = 3.30, p = 0.0012) and YA vs ML (t (138) = 4.09, p = 0.00007). For the Central frequency ratio, we found α/β ratio to vary non-linearly (quadratic) with age (β₁ = -0.0059138, R²=0.61 p = 0.005), whereby first decreases for middle age and subsequently an increase for older age participants suggesting an overall U-shaped response of α/β ratio through lifespan (Figure 8(B)). No significant difference was found between the categorical age groups for θ/α and θ/β peak ratios (Extended Data Figures 8-1, 8-2 and Table 8-1).

Power Ratio of θ/α was found to be positively correlated with age (β₁ = 0.0057613, R²= 0.40, p = 0.02) whereas α/β power ratio was negatively correlated with age (β₁ = -0.018116, R² = 0.85, p = 0.000001) (Figure 8(B)). Significant Categorical difference was found for θ/α power ratio between YA vs OA (t (136) = 4.9615, p = 0.000002), YA vs ME (t (138) = 2.75, p = 0.0067), YA vs ML (t (138) = 4.92, p = 0.000002), ME vs OA (t (134) = 2.24, p = 0.02). No significant correlation was found for θ/β power ratios with age (R² = 0.2, p = 0.1). For α/β power ratio, significant categorical difference was found between YA vs OA (t (76) = -4.6, p = 0.00001), ME vs OA (t (59) = -3.33, p = 0.0015), and ML vs OA (t
(62) = -2.46, p = 0.01). No significant difference was found between the categorical age groups for $\theta/\beta$ power ratio.

Bandwidth ratio of $\theta/\beta$ and $\theta/\alpha$ was found to be negatively correlated with age (Extended analysis is shown in Extended Data Figures 8-3, 8-4). Categorical analysis revealed differences between the YA vs OA ($t \ (80) = 2.21, p = 0.029$) for $\theta/\beta$ bandwidth ratio. No significant difference was found between the categorical age group for $\alpha/\beta$ bandwidth ratio.

After characterising the normative pattern of true oscillatory changes across age, we tested our hypothesis by carrying out regression analysis whereby keeping 1/f noise, periodic features as an explanatory variable and behavioural measures as response variable (see methods). All correlations were performed after regressing out the age.

We first analysed the behavioural responses of the same participants in the visual short term memory task to replicate the well-established cognitive decline with age. Grouping of participants in the age groups and bins were done similarly.

4. Behavioural Results: Age-Related Cognitive decline reflected in Performance

**Precision:** As expected Precision becomes worse with memory load and age. Overall Precision was high for the set size 1 (61.1% SEM 2%) as compared to set size 2 (48.7% SEM 1.9%), 3 (39.6% SEM 1%) and 4 (39% SEM 0.7%). Continuous analysis revealed significant decrease in precision with age in both low and high load conditions (Low load, $r = -0.85, p <0.01$, High load, $r = -0.61, p < 0.05$) (Figure 9 (A), Extended analysis is shown in Extended Data Figure 9-1). Categorical analysis between the groups revealed significant differences in the mean of YA vs OA ($YA = 0.48 \pm 0.008$, OA $= 0.30 \pm 0.005$, p < 0.0001), YA vs ME ($YA = 0.48 \pm 0.008$, ME $= 0.45 \pm 0.007$, p < 0.001), YA vs ML ($YA = 0.48 \pm 0.008$, ML $= 0.43 \pm 0.007$, p < 0.0001), and ME vs OA (ME $= 0.45 \pm 0.007$, OA $= 0.30 \pm 0.005$, p < 0.0001)
groups. Within group analysis also revealed significant increase in Precision with increase in memory load (Extended Data Figure 9-2, Table 9-1)

**Reaction Time:** Overall Reaction time was higher for the set size 4 (910.2 ± 21.6 ms) as compared to set size 1 (878.7 ± 19.9 ms), 2 (870.4 ± 19.9 ms) and 3 (882.6 ± 21.4 ms) but increases significantly with age (Low load (r) = +0.57, p <0.05, High load (r) = +0.56, p <0.05) (Figure 9(B)). Group analysis also revealed significant difference between YA vs OA ( YA = 668 ± 35.4, OA = 1009 ± 38.9, p < 0.00001), YA vs ME ( YA = 668 ± 35.4, ME = 828.8 ± 41.5, p = 0.002), YA vs ML ( YA = 668 ± 35.4, ML = 886 ± 33.4, p < 0.001), ME vs ML (ME = 828.8 ± 41.5, ML = 886 ± 33.4, p = 0.03), ME vs OA ( ME = 828.8 ± 41.5, OA = 1009 ± 38.9, p < 0.001), ML vs OA ( ML = 886 ± 33.4, OA = 1009 ± 38.9, p = 0.05).

**VSTM capacity (k):** VSTM capacity was found to decrease with age (Low load (r) = -0.81 p<0.001, High load (r) = -0.87, p <0.001) (Figure 9(C)). Categorical analysis between the group revealed significant difference between YA vs OA (YA = 1.84 ± 0.01, OA = 1.66 ± 0.02, p < 0.0001), YA vs ML (YA = 1.84 ± 0.01, ML = 1.79 ± 0.01, p = 0.004), ME vs OA (ME = 1.83 ± 0.01, OA = 1.66 ± 0.02, p < 0.0001), and ML vs OA (ML = 1.79 ± 0.01, OA = 1.66 ± 0.02, p < 0.001). (Results for all the set sizes are reported in Extended data Figure 9-4)

**Mean Uncertainty (Metacognitive measure):** Subjective Uncertainty was higher in set 4 (29.7 ± 1) as compared to set size 1 (11.8 ± 0.39), 2 (15.6 ± 0.5) and 3 (20.7 ± 0.67). After performing regression and correlation analysis, we found that subjective uncertainty significantly decreases with age in low load condition (Low load (r) = -0.56, p <0.05) (Figure 9(D)). Suggesting that older adults tend to be more confident about their erroneous answers when the load is less. Categorical analysis revealed significant differences in the mean of YA vs OA (YA = 18.5 ± 0.97, OA = 14 ± 1, p < 0.001), YA vs ME (YA = 18.5 ± 0.97, ME = 16.07 ± 0.95, p = 0.02), YA vs ML (YA = 18.5 ± 0.97, ML = 14.85 ± 1.05, p < 0.001), and ME vs OA (ME = 16.07 ± 0.95, OA = 14 ± 1, p = 0.003). Within group analysis also revealed significant increase in subjective uncertainty with increase in memory load (Extended Data Figure 9-3)
5. Aperiodic 1/f slope: Predictive of all measures of VSTM

We then assessed whether the VSTM performance was impacted by 1/f slope. As hypothesised, RS Aperiodic 1/f noise was found to be predictive of decreased precision (Low Load: \( r = -0.74, p = 0.002 \), High Load: \( r = -0.48, p = 0.08 \)), memory capacity (Low Load: \( r = -0.68, p = 0.0007 \), High Load: \( r = +0.82, p = 0.0003 \)), Mean Uncertainty (Low load: \( r = -0.58, p =0.03 \), High Load: \( r = -0.6, p = 0.02 \)) and increased Reaction Time (Low load: \( r = +0.56, p = 0.00005 \), High load: \( r = +0.57, p = 0.00005 \)) in Visual Short term memory task (Figure 10). However, we did not find any correlation between 1/f offset and behavioural measures (Extended Data Tables 10-1, 10-2). As aperiodic 1/f noise mediated a global effect on the VSTM performance, we further wanted to investigate how different oscillatory components mediate changes in the specific behaviour measures in VSTM performance through lifespan.

6. Precision increases with increase in Alpha power and \( \alpha/\beta \) power ratio

Precision was found to be positively correlated with the alpha power for both low (\( \beta_1 = 0.28077, R^2 = 0.425, p = 0.0115 \)) and high (\( \beta_1 = 0.17617, R^2 = 0.38, p = 0.0186 \)) load condition (Figure 11(A)). \( \alpha/\beta \) Power ratio was also found to be a significant predictor of precision in low (\( \beta_1 = 0.11906, R^2 = 0.69, p = 0.0002 \)) and high load (\( \beta_1 = 0.063459, R^2 = 0.4, p = 0.008 \)) conditions across lifespan (Figure 11(B)). All the regression analysis results are shown for specific oscillatory features with VSTM measures in Extended Data Table 11-1.

7. Speed of Processing predicted by Alpha speed
Speed of Alpha is often related to the speed of processing which is generally measured as reaction time. As we observed that speed of alpha decreases and RT increases with age, we wanted to investigate if this decrease in alpha speed affected the speed of processing in older adults. Alpha Speed significantly predicted the speed of processing for both low ($\beta_1 = -340.82$, $R^2 = 0.43$, $p = 0.0108$) and high ($\beta_1 = -352.41$, $R^2 = 0.39$, $p = 0.0158$) load conditions (Figure 11(C)).

8. VSTM Capacity predicted by Theta power and $\theta / \alpha$ band power ratio

We found a significant negative correlation of VSTM capacity with theta power (Low Load: $r = -0.729$, $p = 0.004$, High Load: $r = -0.679$, $p = 0.01$) and $\theta / \alpha$ power ratio (Low Load: $r = -0.64$, $p = 0.01$, High Load: $r = -0.75$, $p = 0.001$), suggesting that these two play an important role in storing items in working memory. Regression analysis also revealed a significant role of Theta power and $\theta / \alpha$ power ratio in predicting VSTM capacity in low (Theta Power: $\beta_1 = -0.63163$, $R^2 = 0.53$, $p = 0.0046$, $\theta / \alpha$: $\beta_1 = -1.5827$, $R^2 = 0.569$, $p = 0.002$) and High load conditions (Theta Power: $\beta_1 = -1.8862$, $R^2 = 0.46$, $p = 0.011$, $\theta / \alpha$: $\beta_1 = -0.35435$, $R^2 = 0.42$, $p = 0.01$) (Figure 11(D & E) and Extended Data Tables 11-2, 11-3, 11-4).

DISCUSSION

Using three different measures (aperiodic 1/f slope and offset, Peak Frequency (PF) and Band Ratio (BR) of power in various frequencies), we have systematically investigated the spontaneous temporal dynamics and dynamical changes during resting state associated with healthy adult lifespan. Subsequently, we have demonstrated how these measures potentially link distinct behavioural responses during short-term working memory processing. Many previous studies in ageing literature have demonstrated that task-relevant oscillatory changes accurately demarcate task performance in various cognitive domains (Clark et al., 2004; Rondina et al., 2019; Proskovec et al., 2016; Cummins et al., 2007; Tóth et al., 2014). As the resting-state serves as a baseline/control for the diverse task-related changes, it is crucial to characterise how specifically ageing alters the normative brain network dynamics to impact cognition.
The domain general effect of age-associated aperiodic 1/f activity

To track systematically healthy ageing associated changes in neuronal oscillations through lifespan, a substantial number of previous studies have used narrowband power analysis that presumes that spectral power implies oscillatory power, without precisely separating the 1/f activity which in itself is dynamic and it impacts the oscillatory power which can lead to misinterpretation of the results. Extended analysis in Extended Data Figure 3-5 shows the relation between 1/f slope and dominant periodic features, indicating the interdependence of these two components and the necessity to detangle these. We approached this problem by applying a parameterization model (Voytek et al., 2020) which detangles the periodic and aperiodic 1/f component.

Recent studies have considered 1/f slope as an index of “noise” in the brain (Ouyang et al., 2020; Voytek et al., 2020). Ageing is associated with an increase in cortical neural noise, where studies have previously used RT as a proxy for the neural noise (Cremer et al., 1987; Salthous et al., 1985; Welford, 1981). We observed 1/f slope of the MEG spectral power increases with age (flattening of PSD), which is suggestive of increased desynchronised neuronal activity (Hong et al., 2012; Podvalny et al., 2015). Voytek and colleagues had suggested that this flattening of PSD slopes which they indexed for “noise” might be a hallmark of age-related cognitive decline (Voytek et al., 2015). Also, aperiodic 1/f “noise” is found to be very dynamic in nature and it has been shown to be predictive of performance in working memory tasks (Voytek et al., 2015), N400 lexical prediction (Dave et al., 2017) and in grammar learning (Cross et al., 2020). Our results depict the association between global change in the 1/f slope with capacity, speed, precision, and metacognition in short-term working memory processing. As 1/f activity is associated with several distinct domains of cognition, we further suggest that age-related increase in aperiodic 1/f slope does not necessarily mediate any domain-specific processing rather it affects domain general processing (Figure 12).

Additionally, the increase in 1/f slope follows a monotonic non-linear relationship with age suggesting that the rate of change in desynchronised neural activity is not necessarily constant across adult lifespan.
We observe some deviation from the normal trend for both 1/f slope and offset in age-group 60-80, which might be due to the observed increased variance in the older group. Besides, aperiodic 1/f features were found to not only vary across subjects (more for elderly) but also across different sensors indicating substantial variability and idiosyncrasy. Though 1/f slope shows spatial heterogeneity in the young group, such as being less negative in the anterior sensors compared to the posterior sensors, older participants display a more homogenous distribution of less negative 1/f slope values. The broadband offset shows no significant deviation with age, but significant between-group differences were observed.

Aperiodic 1/f activity, self-organized criticality, and nonlinear relationship with adult lifespan

At a more fundamental level, 1/f scale reflects the self-similar temporal properties of the self-organised critical states. Although the aim of this study is not to resolve this debate, however, we argue that 1/f activity could arise from potentially number of factors e.g., altered tissue properties or self-organized criticality and transient stability with ageing and change in underlying excitation-inhibition (E/I) balance (Bedard C. et al., 2006; Voytek et al., 2015; Gao et al., 2017; Naik et al., 2017; Naskar et al., 2021).

Criticality hypothesis, which proposes that the brain operates in a critical state, and alteration in criticality could be symptomatic or causative for certain pathologies (Hesse et al., 2014) seems to be operative here in terms reorganization of brain dynamics based on 1/f slope and offset and their relationship with cognitive performance. Literature suggests that neural networks at criticality exhibit properties for optimal performance such as information transmission & storage, metastable state, dynamic range and computational power (Beggs et al., 2008; Shew et al, 2013). However, 1/f scale cannot alone be explained by criticality; rather emergence may lie in the local tissue properties (Bedard et al., 2006). Healthy ageing is consonant with alteration of physiological properties in brain tissue (Aalami et al., 2003; Peters, 2006), therefore, it seems plausible to say that change in 1/f scale and increase in 1/f slope exhibiting non-linear relationship with ageing has its origin in the local tissue properties.

Subsequently, the association of 1/f slope with cognitive and metacognitive aspects of visual short-term memory demonstrate the domain general effects of local tissue properties affecting self-organized criticality of functional brain states which in turn affects behaviour.
Peak frequency, Band-ratio relates to distinct aspects of memory processing

In oscillatory dynamics, we observe a significant decline in PAF with age as shown by previous studies (Voytek et al., 2015; Sahoo et al., 2020). This decrease in PAF was not found to be localised to specific sensors, rather a global significant decrease was observed (see Fig. 5(B)). The speed of alpha is often associated with the speed of information processing therefore, higher alpha speed is needed for optimal performance in cognitive tasks (Surwillo et al., 1961) and determine the temporal resolution of visual perceptual integration (Samaha et al., 2015). Fig. 11(C) shows that the reaction time of the participants or speed of memory retrieval is well predicted by global alpha speed. Hence, higher the speed of alpha, fast is the retrieval, and consequently lesser reaction time for younger adults. As ageing is characterized by attentional difficulties in particular, a reduced capability to inhibit irrelevant information (McNab et al., 2015), therefore, alpha band power may have an important role in determining how accurately older individual’s recall the memorized items. However, a study by Vaden et al., 2012 demonstrated that older people do not use alpha power suppression to inhibit distractor’s information. In this work, we found that alpha power decreases with age, particularly over occipito-parietal sensors (Fig. 6) which significantly predicts the precision (Fig. 11(A)), along with $\alpha/\beta$ power which decreases with age (Griffiths et al., 2019) (Fig. 8(B)). It plays a crucial role in suppressing irrelevant information, therefore, not being able to ignore distractions might be one of the reasons for low VSTM capacity found in older adults.

The relevance of Theta CF in determining VSTM capacity in a task is well known in the literature. A study by Moran et al., 2010 shows that both slow and fast theta frequencies correlated to the high memory capacity, distributed across different networks. In the context of ageing, we observe that theta CF slightly increases for older subjects as compared to younger adults which may itself affect the storing capacity. There are studies which have observed an increase in RS theta power in older adults (Klimesch et al., 1999 for review; Klass et al., 1995) others have reported theta power decrease in resting as well as in the task with age (Babiloni et al., 2006; Cummins et al., 2007; Leirer et al., 2011; Vlahou et al., 2014).
However, we found an increase in theta power with age, which significantly predicted the VSTM capacity (Fig. 6(A), 11(E)) along with $\theta/\alpha$ power ratio (TAR) which also significantly increases with age (Fig. 8).

Few studies including the study by Trammell et al., 2017 found decreased performance in RM correlated with increased TAR in old adults. We found substantial variability in the presence of theta power in participants. For instance, in young groups, the theta was not observed over frontal and left temporal sensors, whereas in older participants the theta power was observed only over temporal sensors.

Additionally, we also observed an increase in Beta power with age which is well reported in the literature, generally associated with the movement-related activity (Ishii et al., 2017; Sahoo et al., 2020) but we also observed a significant decrease in beta peak frequency with age which was more localised to the central-parietal sensors (generally found in depression and other psychological disorders’ patients in open-eye condition; Roohi-Azizi et al., 2017). In the bandwidth measure, only Beta bandwidth was found to increase significantly with age which indicates higher variability in beta frequency (Fig. 7). This increase was mostly observed in the central and temporal sensors. Differences in the regional attenuation of absolute and relative beta power within specific high frequency bands may reflect the disparate neuropathologic processes of mild cognitive impairment associated with age, as well as the extent of brain dysfunction. We can further speculate the amount of spread of power in a particular frequency range that increases with age may suggest a state of fractured synchronization in elderly compared to younger adults. Mechanistically, this can be a result of decreased myelination in long-range fibres across ageing (which introduces time-delays in the resultant dynamical system governing such processes. Time delays are known to introduce phase lags in a group of coupled (and synchronized) oscillators resulting in lowering of synchronization indices such as increased band width.

In conclusion, our results suggest that the age-associated change in aperiodic 1/f activity affects the global information processing and links with speed of information processing, cognitive capacity, precision, and metacognitive awareness (all behavioural measures). In contrast, periodic features; PF and BR of different frequency bands relate to more local processing and selective behavioural measures in VSTM task crucially impacting distinct aspects of memory processing with age. On that account, we suggest that the
change observed in local tissue properties with ageing is reflected as the global increase in aperiodic 1/f slope. This increase in 1/f slope seems to impact distributed processes of cognition as it alters the self-organised critical functional brain states, whereas oscillatory features mediate localised processing, that is relevant for the specific task (Figure 12).

An important limitation of our study is that we have only tested aperiodic 1/f slope-offset, and periodic features PF and BR based on VSTM task, therefore, further investigation is warranted relating the RS 1/f slope-offset, PF, BR with the performance in different cognitive tasks (e.g., lexical processing, episodic memory encoding and retrieval, emotion regulation, fluid and crystallized intelligence). Additionally, we have also not looked at these three measures trial-wise instead related resting state brain dynamics (periodic and aperiodic) with behavioural responses from the same participants. Another major limitation was posed by the Cam-CAN dataset, because of the presence of harmonics of lower frequencies in higher frequencies, we were not able to systematically tease apart the effect of 1/f activity on gamma-frequency band. From a recent study employing visual steady state response task it has been shown gamma band power systematically weakens with age which may have a crucial impact on attentional processing (Murty et al., 2020). Lastly, we still do not know which sources are responsible for 1/f baseline shift and is currently investigated in a separate future work, where source reconstruction and applying computational modelling on the source level data give us mechanistic understanding about the generative processes.

Despite these limitations, we think there is no loss of generality by focusing on visual short-term working memory processing task alone as age-associated change in aperiodic 1/f activity is pervasively present in all goal directed tasks and same for oscillatory changes quantified by PF and BR. Therefore, all these three normative measures proposed in this study together can track vast majority of alterations associated with healthy and atypical neurodevelopment and healthy and pathological ageing conditions under a variety of task settings which is important for developing non-invasive biomarker in future clinical applications.
Table Legends

TABLE 1: Each representative age is divided into four groups Young Adults (YA), Middle Elderly (ME), Middle Late (ML), Old Adults (OA)

TABLE 2: Estimated behavioural measures of VSTM task

TABLE 3: Effect of Age on Periodic and Aperiodic Features

Figure Legends

Figure 1. Experimental design of the colour recall task
Example trial, with memory load of 4 items. (Data were taken from Cam-CAN repository; Adapted from Mitchell et al., (2018)).

Figure 2. Data processing and analyses pipeline

Figure 3. Parameterization using FOOOF Model
(A) Power Spectrum of all age-groups after removing the 1/f activity component (B) & (C) FOOOF Model fit for Young and Old Adults. Power spectrum without model fitting and for the other two age categories along with their statistics is shown in Extended Data Figure 3-1. Other extended analysis for different age groups is shown in Extended Data Figures 3-2, 3-3, 3-4, 3-5.

Figure 4. Aperiodic 1/f Slope and Offset
(A) Left: 1/f slope as a function of age. Right: 1/f slope for four age groups. (B) Left: 1/f Offset as a function of age. Right: 1/f Offset for four age groups. ‘r’ represents the correlation value. The dashed line represents a linear regression fit. Error bar denotes SEM. (C)(D) Aperiodic 1/f slope and 1/f offset spatial topography for Young (YA) and Old (OA). Clusters of sensors with significant positive and negative differences in 1/f slope and 1/f offset between the OA and YA group are represented with black and white dots, respectively.
Figure 5. Alpha and Beta peak frequency as a function of Age

(A) Top: PAF as a function of age. Bottom: Beta peak frequency with age. ‘r’ represents the correlation coefficient. The dashed line represents a linear regression fit. Error bar denotes SEM. (B) Top: Spatial Topography for PAF and Beta peak frequency for Young (YA) and Old (OA). Clusters of sensors with negative differences which contribute to the decrease are represented as white dots. Dominant frequency and power for YA and OA are shown in Extended Data Figure 5-1.

Figure 6. Parameterised Global Power as a Function of Age

(A) Increase in Theta and Beta power whereas a decrease in Alpha power with Age. Error bar represents SEM. (B) Spatial Power topography of Theta, Alpha and Beta for young (YA) and old adults (OA). Clusters of sensors with significant positive and negative differences between the OA and YA group are represented with black and white dots, respectively. Frequency specific power as a function of age across different sensors is shown as Extended Data in Figure 6-1.

Figure 7. Global frequency-specific Bandwidth with Age

(A) Bar graph for each age group, representing bandwidth for each frequency band. (B) Spatial topography of Beta BW for young (YA) and old adults (OA). Clusters of sensors with significant positive and negative differences between the OA and YA group are represented with black and white dots, respectively. All the extended analysis are shown as Extended Data in Figures 7-1, 7-2.

Figure 8. Spatial topography of band-ratio measures as a function of age

(A) Spatial topography of Alpha/Beta peak frequency ratio ($\alpha/\beta$ CF) (top), Alpha/Beta power ratio ($\alpha/\beta$ PW) (centre) and Theta/Alpha power ratio ($\theta/\alpha$) (bottom) for young (YA) and old adults (OA). (B) Regression fit model for each of the ratio measures keeping age as an explanatory variable. Error bar represents SEM. $R^2$ represents goodness of fit and ‘r’ represents the correlation coefficient. All the
Figure 9. Effect of Memory load and Age on VSTM.

VSTM measures (A) Precision (B) Reaction time (C) VSTM capacity (k) (D) Mean Uncertainty as a function of age. Low load and high load indicate set size 2 and 4 respectively. The dashed line represents the linear regression fit. Error bar represents the SEM for each age bin. Asterisks indicate significance.

All the extended analysis are shown as Extended Data Figures 9-1, 9-2, 9-3, 9-4 and Table 9-1.

Figure 10. Aperiodic 1/f slope mediating VSTM performance.

Linear regression model for VSTM measure (A) Precision (B) Reaction time (C) VSTM capacity (k) (D) Mean uncertainty as a response variable and aperiodic 1/f slope as an explanatory variable, after regressing out the age effect. The dashed line represents linear regression fir. Error bar represents SEM. Low load and high load indicates set size 2 and 4 respectively. ‘r’ is Pearson's coefficient. All the extended analysis are shown as Extended Data Tables 10-1, 10-2.

Figure 11. VSTM measures predicted by different oscillatory features and 1/f offset.

(A) & (B) Precision predicted by global Alpha power and $\alpha/\beta$ Power Ratio. (C) Speed of Processing (RT) well predicted by global alpha speed (PAF). (D) & (E) VSTM capacity predicted by global theta power and $\theta/\alpha$ Power Ratio. Age is regressed out. Low load and high load indicate set size 2 and 4 respectively. The dashed line represents the regression line. Error bar represents SEM. ‘r’ corresponds to Pearson's coefficient. All the extended analysis are shown as Extended Data Tables 11-1, 11-2, 11-3, 11-4.

Figure 12. (Left) Aperiodic 1/f slope index behavior in distinct cognitive domain: Aperiodic 1/f slope increases globally which is reflected in performance in different cognitive tasks which includes VSTM
task precision, cognitive capacity, reaction time and metacognition and in other cognitive tasks (N900 lexical prediction, working memory, grammar learning) reported previously. ‘r’ represents the Pearson’s correlation coefficient. *(Right) Periodic features index task specific behavioral measures:* Periodic features (CF,BW,PW,BR) are more task specific in nature. After regressing out the age, Alpha band power, Alpha/Beta band ratio index for precision; Theta/Alpha band ratio, Theta power index for cognitive capacity; Alpha central frequency index for reaction time. ‘r’ represents the Pearson’s correlation coefficient.

Extended Data Legends

Table 8-1 Regression table for global frequency band-ratios with Age. F-value, Beta coefficient, Goodness of fit and significance of the model is reported.

Table 9-1: Regression table for VSTM measures with Age. F-value, Beta coefficient, Goodness of fit and significance of the model is reported.

Table 10-1: Regression table for VSTM measures with aperiodic slope. F-value, Beta coefficient, Goodness of fit and significance of the model is reported.

Table 10-2: Regression table for VSTM measures with Aperiodic 1/f offset. F-value, Beta coefficient, Goodness of fit and significance of the model is reported.

Table 11-1: Regression table for specific oscillatory features with VSTM measures. F-value, Beta coefficient, Goodness of fit and significance of the model is reported.

Table 11-2: Regression table for $\alpha/\beta$ CF with VSTM measures. F-value, Beta coefficient, Goodness of fit and significance of the model is reported.

Table 11-3: Regression table for $\alpha/\beta$ Power ratio with VSTM measures. F-value, Beta coefficient, Goodness of fit and significance of the model is reported.

Table 11-4: Regression table for $\theta/\alpha$ Power ratio with VSTM measures. F-value, Beta coefficient, Goodness of fit and significance of the model is reported.

Figure 3-1. (A) Power spectrum without model fitting (B) & (C) FOOOF- Power spectrum model for ME and ML age groups, along with its statistics.

Figure 3-2. Power Spectrum in log-log space
Figure 3-3. (A) Aperiodic component of different age groups (B) Boxplot of aperiodic features across different age groups derived from the component.

Figure 3-4. Variability of aperiodic component across individual subjects in each age group.

Figure 3-5. Association between 1/f aperiodic slope with periodic components of the dominant oscillations.

Figure 5-1. Dominant frequency (A) and respective power (B) for YA and OA.

Figure 6-1. Frequency specific power as a function of age across different sensors. For Frontal sensors, theta power is not shown as only few age groups showed peaks in theta range. Error bar represents SEM.

Figure 7-1. Frequency specific bandwidth for different age groups.

Figure 7-2. Spatial topography of Theta Bandwidth (A) and Alpha Bandwidth (B) for YA and OA.

Figure 8-1. (A) Theta/Alpha peak frequency ratio and (B) Theta/Beta peak Frequency ratio for YA and OA.

Figure 8-2. Theta/Beta power ratio for YA and OA.

Figure 8-3. (A) Theta/Beta Band Width (B) Theta/Alpha Band Width as a function of age.

Figure 8-4. Topoplots of (A) Theta/Beta Band Width (B) Theta/Alpha Band Width for YA and OA.

Figure 8-5. Association between 1/f slope with Alpha/Beta power ratio.

Figure 9-1. VSTM measures as a function of age. Participants with same age were grouped together (dots), size of the dot represents the SEM of the group. Shaded area is the 95% confidence interval.

Figure 9-2. Precision across age groups and set size.

Figure 9-3. Uncertainty across age groups and set size.

Figure 9-4. VSTM capacity across age groups for different set sizes.

References


**TABLE 1**: Each representative age is divided into four groups Young Adults (YA), Middle Elderly (ME), Middle Late (ML), Old Adults (OA).
<table>
<thead>
<tr>
<th>S.No.</th>
<th>Group</th>
<th>Age</th>
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<tbody>
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<td>Young Adults (YA)</td>
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<td>70</td>
</tr>
<tr>
<td>2.</td>
<td>Middle Elderly (ME)</td>
<td>36-50</td>
<td>70</td>
</tr>
<tr>
<td>3.</td>
<td>Middle-Late (ML)</td>
<td>51-65</td>
<td>70</td>
</tr>
<tr>
<td>4.</td>
<td>Old Adults (OA)</td>
<td>66-88</td>
<td>70</td>
</tr>
</tbody>
</table>

**TABLE 2**: Estimated behavioural measures of VSTM task

<table>
<thead>
<tr>
<th>S.No</th>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Precision</td>
<td>Accuracy of reportable items (degrees⁻¹)</td>
</tr>
<tr>
<td>2.</td>
<td>RT</td>
<td>Median Reaction time (ms)</td>
</tr>
<tr>
<td>3.</td>
<td>K(VSTM Capacity)</td>
<td>Number of reportable items (k-score)</td>
</tr>
<tr>
<td>4.</td>
<td>Mean Uncertainty</td>
<td>Size of confidence interval within which answer is thought to lie (degrees)</td>
</tr>
</tbody>
</table>

**TABLE 3**: Effect of Age on Periodic and Aperiodic Features
<table>
<thead>
<tr>
<th>Effect</th>
<th>Response Variable</th>
<th>F-value</th>
<th>Coefficient $b_1$</th>
<th>R$^2$</th>
<th>p-value</th>
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</thead>
<tbody>
<tr>
<td><strong>Aperiodic Features</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1/f Slope</td>
<td></td>
<td>26</td>
<td>+0.0034901</td>
<td>0.584</td>
<td>0.003262</td>
</tr>
<tr>
<td>1/f Offset</td>
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<td>5.35</td>
<td>-0.0033423</td>
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<td>0.0894</td>
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<td></td>
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<tr>
<td>Power</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Theta</td>
<td></td>
<td>6.82</td>
<td>+0.0050947</td>
<td>0.363</td>
<td>0.0227</td>
</tr>
<tr>
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<td>36.3</td>
<td>-0.0059263</td>
<td>0.751</td>
<td>0.0000599</td>
</tr>
<tr>
<td>Beta</td>
<td></td>
<td>28.7</td>
<td>+0.002496</td>
<td>0.705</td>
<td>0.000172</td>
</tr>
<tr>
<td><strong>Central Frequency</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Theta</td>
<td></td>
<td>0.577</td>
<td>+0.0029928</td>
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<td>7.32</td>
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<tr>
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<td>0.58</td>
<td>0.00141</td>
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**Figure 1.**
Figure 2.

MEG DATA
8mins Resting State Data
102 Sensors

PRE-PROCESSING
Head motion correction, noise channel rejection, EOG & ECG channel removal, ICA correction, downsample (250Hz)

POWER SPECTRUM
Sensor Level

Model Description

MEASURES
Precision
Capacity
Reaction Time
Metacognition

COGNITIVE PERFORMANCE
Visual short-term Memory

Low Load
n = 2
High Load
n = 4

REGRESSION MODEL
Linear & Non-linear

FEATURE EXTRACTION
Power (PW)
Central Frequency (CF)
Bandwidth (BW)
1/f Slope
1/f Offset

FOOOF MODEL

\[
P = L + \sum \frac{G_c}{\exp\left(\frac{F-c}{\alpha}\right)}
\]

\[
L = b - \log(1 + F)
\]
Figure 3.
Figure 4.
Figure 5.
Figure 6.
Figure 7.
Figure 8.
Figure 9.
Figure 10.
Figure 11.
Figure 12.
Table 1:

<table>
<thead>
<tr>
<th>S.No.</th>
<th>Group</th>
<th>Age</th>
<th>N</th>
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<tbody>
<tr>
<td>1.</td>
<td>Young Adults (YA)</td>
<td>18-35</td>
<td>70</td>
</tr>
<tr>
<td>2.</td>
<td>Middle Elderly (ME)</td>
<td>36-50</td>
<td>70</td>
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