



Power and temporal dynamics of alpha oscillations at rest differentiate cognitive performance involving sustained and phasic cognitive control



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ABSTRACT

Resting state neuronal activity in EEG/MEG recordings is primarily characterized by the presence of alpha oscillations (approx. 8–12 Hz). However, their functional significance and link to cognitive task performance remains elusive. We investigated resting state neuronal activity and its relation to task performance by assessing traditional measures of alpha activity (power and individual alpha peak frequency) and dynamic properties of the signal measured by long-range temporal correlations (LRTC). Multichannel EEG was recorded at rest in 82 healthy male adults and compared to their cognitive performance, measured by tests involving executive functions, working memory, short- and long-term memory demands. Our results showed that attention-span scores positively correlated with alpha power at rest, with corresponding neuronal sources located primarily in the left-hemispheric anterior cingulate cortex, parietal regions, and bilateral supplementary motor areas. Furthermore, better working memory performance was related to increased LRTC of alpha oscillations at rest in the right hemispheric fronto-parietal, temporal, and occipital regions. Our findings suggest that resting state neuronal activity may reflect properties of brain networks that are functionally relevant for cognitive task performance. While alpha power measured at rest might relate to tasks that employ sustained inhibitory control, LRTC are suggested to reflect the capacity of neuronal networks to perform tasks that require phasic attention and quick adaptation to changing task demands.

1. Introduction

While resting state (RS) on a behavioral level refers to a subject's state without any explicit cognitive or motor task and is associated with mind-wandering, on a neurophysiological level it is characterized by complex spatio-temporal patterns of neuronal interactions in the brain (Bazanava, 2012; Raichle, 2010; Raichle and Snyder, 2007). At the same time RS neuronal dynamics demonstrate test-retest reproducibility and

heritability (Diaz et al., 2013; Linkenkaer-Hansen et al., 2007; Smit et al., 2005; Nikulin & Brismar, 2004). Importantly, previous studies have also revealed similarities between RS neuronal dynamics and task-related activity: Functional networks, involving fronto-parietal networks, continuously interact in patterns that correspond to those expressed during task performance (Becker et al., 2018; Tavor et al., 2016; Smith et al., 2009; De Luca et al., 2006). Given these findings of topographic resemblance of neuronal activity at rest as well as during task, we aimed

Abbreviations: ACC, anterior cingulate cortex; DFA, Detrended Fluctuation Analysis; CVLT, California Verbal Learning Test; CO, cingulo-opercular; EEG, electroencephalography; FP, fronto-parietal; IAF, individual alpha peak frequency; lLING, left lingual gyrus; lPoCG, left postcentral gyrus; LRTC, long-range temporal correlations; MEG, magnetoencephalography; rLOC, right lateral occipital cortex; rPreCG, right precentral gyrus; RS, resting state; rSFG, right superior frontal gyrus; rSMG, right supramarginal gyrus; RT, reaction time; rTG, right temporal gyrus; SMA, supplementary motor area; SPL, superior parietal lobule; SVD, Singular Value Decomposition; TAP, Test of Attentional Performance; TMT, Trail Making Test.

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to further investigate whether RS neuronal dynamics might also be linked to differences in cognitive task performance. Consequently, demonstrating such a functional relationship might contribute to further understanding of neuronal parameters defining individual variability in task performance.

In humans, the most prominent RS oscillatory activity is marked by a pronounced power in the alpha frequency band (approx. 8–12 Hz; Bazanova and Vernon, 2014; Romei et al., 2008; Pfurtscheller & Lopes da Silva, 1999). The precise functional role of oscillatory alpha power, however, remains a topic of active research. It has been linked to idling (Pfurtscheller et al., 1996), cortical inhibition by top-down control (Klimesch et al., 2007), and gating mechanisms (Jensen and Mazaheri, 2010). Furthermore, alpha power and individual alpha peak frequency (IAF) were previously shown to relate to a variety of cognitive tasks, not only during task performance but also when measured at rest (Sadaghiani and Kleinschmidt, 2016). These measures have been found to positively correlate with attention (power and IAF: Klimesch, 1997), short-term memory (power: Prat et al., 2016; Klimesch, 1999; Vogt et al., 1998), working memory (IAF: Clark et al., 2004), and intelligence (power and IAF: Grandy et al., 2013; Thatcher et al., 2005; Doppelmayr et al., 2002).

Notably, alpha power and IAF, used in aforementioned studies, can be considered as rather “static” measures of neuronal activity, typically compressed across several minutes (Bazanova and Vernon, 2014; Bazanova, 2012; Klimesch et al., 2007). In addition, temporal dynamics in the ongoing amplitude of alpha oscillations can be measured across different timescales by assessing long-range temporal correlations (LRTC; Palva et al., 2013; Linkenkaer-Hansen et al., 2007; Nikulin & Brismar, 2005, 2004; Linkenkaer-Hansen et al., 2001), subsequently referred to as a “dynamic” measure in the present study. LRTC were previously suggested to characterize neuronal network activity near a critical state (Meisel et al., 2017; Palva et al., 2013; Nikulin & Brismar, 2004; Linkenkaer-Hansen et al., 2001), which reflects a balance between excitation and inhibition (Poil et al., 2012). This balance in turn was proposed to be optimal for information processing in neuronal networks (Beggs and Plenz, 2004; Shew and Plenz, 2013; Shew et al., 2011) and consequently for task performance: Higher scaling exponents measured at alpha oscillations at rest were previously shown to relate to shorter reaction times in an attention task (Irrmischer et al., 2017) and more adaptive decision making (Colosio et al., 2017). Yet, given that LRTC are likely to reflect neuronal network activity in an optimal state of information processing, we were particularly interested in investigating the relation between LRTC and cognitive performance of higher-order cognitive tasks involving domain-general cognitive control components (Friedman and Miyake, 2017; Kane et al., 2007, 2004). In addition, the novelty of our study also lies in controlling for task heterogeneity (as suggested by Friedman and Miyake, 2017) by employing diverse tasks that involved several sensory modalities (visual and auditory) and different types of stimuli (numeric and verbal).

We utilized three tasks that reflect both unifying (domain-general) and diverse (task-specific) factors of cognitive performance involving executive functions, working memory, short- and long-term memory demands. On a behavioral level, such tasks were previously found to share a common domain-general component referred to as executive attention (McCabe et al., 2010), executive control (Hughes et al., 2014; Miyake et al., 2000) or central executive (Sauseng et al., 2005; Pavlov and Kotchoubey, 2017) - often suggested to be relevant for maintaining and managing task-related goals regardless of a modality employed by a task (Friedman and Miyake, 2017; Unsworth and Engle, 2007; Conway et al., 2001). Moreover, on a neurophysiological level, several studies were able to show that this domain-general component was strongly associated with the activity in frontal (Gazzaley & D'Esposito, 2006; Miyake et al., 2000) and fronto-parietal networks (Pavlov and Kotchoubey, 2017; Zanto and Gazzaley, 2013; Sauseng et al., 2005), which were previously found to relate to cognitive control (Gazzaley & D'Esposito, 2006).

The primary aim of the present study was thus to link properties of RS

neural network activity to cognitive performance. Taking into account previous evidence on alpha power and IAF relating to domain-general constructs (i.e., intelligence; Grandy et al., 2013; Thatcher et al., 2005), and evidence on LRTC reflecting an optimal state for information transmission, we were particularly interested in studying domain-general aspects of cognitive performance and relating them to measures of neuronal activity at rest. For this purpose, we used different cognitive tasks that were previously found to relate to each other, suggesting the common underlying ground (e.g., Hughes et al., 2014; Miyake et al., 2000). We linked cognitive performance scores to alpha band measures that reflected static and dynamic properties of RS alpha activity. Taking into account considerations presented above, we hypothesized that higher alpha power, IAF, and LRTC measures at rest relate to better task performance in all of the tasks, consequently reflecting domain-general components of cognitive performance. We also expected that the strongest associations between oscillatory alpha activity and task performance would be observed primarily in fronto-parietal networks.

2. Materials and methods

Data from the “Leipzig Study for Mind-Body-Emotion Interactions” (LEMON; Babayan et al., 2018, under review), part of the MPI Leipzig Mind-Brain-Body database, were used for the present study.

2.1. Participants

Participants were recruited through public advertisements, leaflets, online advertisements, and information events. Eligibility for the LEMON study was based on the applicants being in good health, not on any medication, no substance abuse, and having no history of neurological diseases. In order to have a homogenous sample, data of 87 healthy right-handed male participants that had EEG recordings were analyzed (the decision was based on previous findings suggesting sex-related differences in neuronal dynamics, resting state functional connectivity and possible hormonal level fluctuations; Filippi et al., 2013; Cahill, 2006; Nikulin & Brismar, 2005). Due to technical difficulties, EEG recordings of five participants were excluded from further analysis, resulting in a sample of 82 participants (age range 20–35 years, mean age = 25.3, SD = 3). Participants provided written informed consent and received monetary compensation. The study protocol was approved by the ethics committee at the medical faculty of the University of Leipzig (reference number 154/13-ff).

2.2. Study design

The participants completed two assessment sessions over two days, each lasting approximately four hours. The first assessment day included a cognitive test battery, and RS electroencephalographic (EEG) data were acquired on the second day. RS recordings consisted of 16 blocks, each lasting 1 min of intermittent eyes closed and eyes open conditions, summing up to a total duration of 8 min per condition. In the present study the eyes closed condition was selected for further analysis, due to a high signal-to-noise ratio at alpha frequency range (Bazanova and Vernon, 2014) and for reflecting a baseline level of neuronal activity that was not contaminated by pronounced stimuli processing. Finally, we also chose the eyes closed condition in order to be able to compare our results to the previous studies (e.g., Prat et al., 2016; Thatcher et al., 2005; Doppelmayr et al., 2002). The acquired RS-EEG data were analyzed together with three tests from the cognition test battery described below.

2.3. Cognitive tests

2.3.1. Trail Making Test

We used the Trail Making Test (TMT; Reitan, 1992) trail B in the present study in order to examine executive functioning and set shifting (Shibuya-Tayoshi et al., 2007). In the TMT trail B, a participant is

presented with a sequence of randomly distributed numbers and letters on a sheet of paper, which have to be connected by using a pencil. The connections should be made in an ascending order and matched alphabetically (e.g., 1-A-2-B-...). Whenever an error is made, a participant is stopped by a researcher and asked to continue from where the error occurred. The total amount of time it takes to complete the trail correctly defines an estimate of performance. Nine participants that performed TMT trail B had to be removed from further analysis due to the misunderstanding of the task and, therefore, seventy-eight participants were further analyzed.

2.3.2. Test of Attentional Performance (TAP)

2.3.2.1. Alertness (TAP: Alertness). The Alertness subtest of the Test of Attentional Performance (TAP; orig. “Testbatterie zur Aufmerksamkeitsprüfung”; version 2.3; Zimmermann and Fimm, 2012) measures alertness and reaction speed, which are estimated after each button press to every stimulus that appears on a screen (the stimulus was marked as a cross in the middle of the screen). We used mean reaction times over all trials as a measure of individual reaction time in order to calculate the switch-cost score described below.

2.3.2.2. Working memory (TAP: working memory). The Working Memory subtest of the TAP (version 2.3; Zimmermann and Fimm, 2012) corresponds to a numeric 2-back task. In total, 100 numbers are presented to a participant who is asked to press a button when a displayed number matches the one 2 steps back. The total amount of possible correct answers is 15.

We calculated the switch-cost score according to the procedure introduced by Hughes et al. (2014) that was originally used to evaluate task-switching. This measure indicates how well a subject can switch between withholding from responding in incongruent trials and answering in congruent trials. According to the procedure, switch-cost builds upon a composite score calculated by ranking the difference between reaction times (RT) of congruent trials (switch trials) and mean RT (derived from TAP: Alertness) into deciles among all participants. An additional 20 points are added to the score for every omission error a participant made. This score incorporates both reaction times and accuracy and was previously shown to correlate strongly with other working memory tasks (Draheim et al., 2016).

Due to a misunderstanding of a task or uncorrected vision, three subjects who completed the TAP: Alertness and TAP: Working memory subtests had to be removed from further analysis, which resulted in a sample of seventy-seven subjects.

2.3.3. California Verbal Learning Test (CVLT-II)

The California Verbal Learning Test (CVLT-II; Niemann et al., 2008) measures short-term and long-term memory processes. A researcher reads a 16-word list (list A) to a participant 5 times, which the participant has to recall after each presentation. The number of correctly recalled words is counted after the first and the fifth round. The test also involves an interference task with another list of 16 words (list B) read only once, which has to be immediately recalled and is followed by the recall of list A (short-delay recall). Long-term memory processes are considered to be employed when participants are asked to recall list A after a 20-min delay firstly without any cues and later arranging the words into 4 different categories (long-delay recall with and without cues; Donders, 2008). During this delay the participants performed other tasks from the cognition battery.

Three subjects who completed the CVLT-II test had to be removed due to missing values or because a different version of the test was used to collect data, which resulted in a sample of eighty-one participant. Raw data scores were transformed then to standardized scores based on age and education (Niemann et al., 2008).

To analyse the data of this test, we used the most statistically robust

four-factor model introduced by Donders (2008; subsequently tested by Carlew et al., 2018; DeJong and Donders, 2009). For the current study we grouped the obtained variables into two scales described in the model, representing attention span and delayed memory performance. The *attention-span* score was calculated as the sum of words recalled after the first presentation of list A and list B, and it was suggested to reflect the ability to encode incoming information after a single presentation of a list subsequently reflecting short-term memory performance (DeJong and Donders, 2009; Donders, 2008). The *delayed memory* score consisted of the sum of words recalled after a short and a long delay with and without cues, and it was suggested to reflect consolidated information retrieval (DeJong and Donders, 2009; Donders, 2008).

2.4. Correlation analysis of cognitive tests

We applied a correlation analysis between the four cognitive test scores in order to interpret a potential domain-general component. For this purpose we used Spearman's rank correlations and corrected it for multiple comparisons using the Bonferroni method (Bland and Altman, 1995).

2.5. EEG recordings

EEG (BrainVision ActiCAP; Brain Products GmbH, Munich, Germany) during RS was recorded in an acoustically shielded room using 62 active electrodes placed according to the international 10–20 system (Oostenvelde and Praamstra, 2001), all referenced to the FCz electrode. Electrooculographic activity was recorded with one electrode placed below the right eye and the ground electrode was placed on the sternum. Electrode impedance was kept below 5k Ω . During data acquisition EEG signals were online band-pass filtered between 0.015 Hz and 1 kHz and digitized at the sampling rate of 2500 Hz. The amplifier was set to 0.1 μ V amplitude resolution.

2.6. EEG pre-processing

EEG data were pre-processed using the EEGLAB toolbox (version 14.1.1b; Delorme and Makeig, 2004) and custom Matlab (MathWorks, Inc, Natick, Massachusetts, USA) scripts. First, EEG data were band-pass filtered between 1 and 45 Hz (4th order, forward and backward directions, Butterworth filter) and downsampled to 250 Hz. The rest conditions with eyes closed were extracted and concatenated to form 8-min blocks. Artefactual channels and data segments were removed after visual inspection. Principal component analysis was used to reduce data dimensionality to N components ($N \geq 30$) that explained 95% of the total variance. Subsequently, data of low dimensionality were then subjected to independent component analysis (Infomax; Bell and Sejnowski, 1995) in order to remove artefacts due to ocular, muscular, and cardiac activity. Data were re-referenced to a common average reference before further analysis.

2.7. Sensor space analysis

2.7.1. Power and peak frequency

Alpha power was calculated in all electrodes as a mean of the squared signal obtained after filtering in 8–12 Hz frequency range.

IAF was determined in all electrodes at the frequency range of 7.5–13 Hz by localizing the frequency at which alpha peak occurs.

2.7.2. LRTC: detrended fluctuation analysis

LRTC were assessed by detrended fluctuation analysis (DFA) in the amplitude envelope of neuronal oscillations, according to procedures described by Hardstone et al. (2012). DFA was performed on the artifact-free, continuous signals while ensuring that the windows did not contain boundaries after 1 min data block concatenation, and/or artifact rejection. We extracted the amplitude envelope from the pre-processed

and filtered alpha band (8–12 Hz) signal for each channel using the Hilbert transform, and the cumulative sum was then calculated:

$$Y(t) = \sum_{i=1}^N a(t)$$

, where $a(t)$ was the amplitude envelope of alpha oscillation at time 't'.

The signal was then split into 30 time windows varying from 3 to 50 s distributed evenly on a logarithmic scale. The shortest window of 3 s was selected in order to avoid spurious correlations due to signal filtering, and the longest window was 50 s in order to obtain sufficiently large number of segments (i.e., approximately 10 segments; cf. Nikulin & Brismar, 2004; Hu et al., 2001). The integrated signal $Y(t)$ was detrended before calculating its fluctuation function $F(\tau)$ for each time window size:

$$F^2(\tau) = \frac{1}{N} \sum_{i=1}^N [Y(t) - Y_i(t)]^2$$

, where τ was a window size and N was the number of samples in the window size.

Using double logarithmic axes, the mean $F(\tau)$ was plotted as a function of window sizes τ and the slope of the least-squares line indicated the scaling exponent ν quantifying LRTC. An exponent of $\nu = 0.5$ reflected uncorrelated signals (i.e., resembling white noise), while an exponent between $0.5 < \nu < 1$ showed persistent autocorrelation and thus the presence of LRTC (Hardstone et al., 2012).

2.8. Source reconstruction and source space analysis

For all subjects, the “New York Head”, a standard highly-detailed forward model of an extended ICBM anatomy (Huang et al., 2016), was used to solve the forward model. The corresponding cortical surface was downsampled to around 2000 vertices, and the leadfield was computed between these cortical sources and channels. Source activity was reconstructed with the free-orientation model using exact low resolution tomography (eLORETA, Haufe and Ewald, 2016; Pascual-Marqui, 2007). We used eLORETA Matlab implementation as a part of M/EEG Toolbox of Hamburg (METH).

2.8.1. Source power and LRTC calculation

Source time series were filtered in alpha frequency range and singular value decomposition (SVD) was applied to each voxel's three-dimensional time course. The first component of SVD, representing the dominant orientation at each voxel, was used for source power and LRTC calculation. The calculation was done in a similar way to that performed in the sensor space.

Alpha power and LRTC values measured at source space were correlated with the performance scores obtained from the cognitive tests described above. For reporting source results, 96 cortical structures were labeled using the Harvard-Oxford cortical atlas (Desikan et al., 2006).

2.8.2. Statistical analysis

Relations between all cognitive test scores and three measures of RS alpha oscillations (power, IAF, LRTC) were calculated using the non-parametric Spearman's rank correlation. In order to account for multiple comparisons we used cluster statistics (Maris and Oostenveld, 2007). Clusters in sensor space were defined as two or more neighbouring channels that demonstrated a significant correlation with $p < 0.05$. Source space clusters were determined from spatially connected vertices on the cortical surface, where correlations passed $p < 0.01$ criterion. Identified sensor/source space clusters were then considered for cluster-based analysis. A null distribution was generated using the Monte Carlo method from 1500 permutations of the original data. In order to correct for multiple comparisons across different test scores ($N = 4$), we used Bonferroni correction (Bland and Altman, 1995).

3. Results

In the first section we report behavioral results of cognitive testing. We later describe findings that relate EEG measures obtained at rest to the task performance.

3.1. Cognitive performance

Data obtained from the four test scores (TAP: Working memory, TMT trail B, CVLT-II: Attention span and Delayed memory) defined cognitive performance. The score distributions and results of the correlation analysis among test scores are displayed in Fig. 1.

The correlation matrix revealed that while several tests correlated with each other, these relationships were either weak (between TAP: Working Memory, TMT: trail B and CVLT-II: Delayed Memory, $\rho = -0.31$) or moderate (between two CVLT-II subscales, attention span and delayed memory, $\rho = 0.43$). The magnitude of the latter correlation was expected, since the same list of words was recalled in the attention-span scale as well as in the delayed memory scale. No significant correlations were observed between tests measuring executive and working memory functions (i.e. TMT trail B, TAP: Working memory), and attention-span task (measured with CVLT-II).

3.2. Resting state EEG measures

Scalp topographies depicting the grand-average of the alpha band measures (power, IAF, and LRTC) across subjects are displayed in Fig. 2. The power of alpha oscillations showed a maximum over occipitoparietal areas, with grand-average values of $17.5 \mu\text{V}^2$ (SEM = 20.12; Fig. 2 [A]). The grand-average IAF was 10.5 ± 0.8 Hz, showing larger values at the occipital regions (Fig. 2 [B]).

Topographies of the scaling exponent (ν , indicating LRTC) had higher values at occipital and parietal areas, yet spreading towards central, centro-frontal and temporal regions (Fig. 2 [C]) compared to the power topography. The average scaling exponent was 0.7 ± 0.07 and the goodness of fit was on average 0.99 ± 0.01 , thus confirming the presence of LRTC extending for up to 50 s. Two examples of the individual differences in scaling exponents from this dataset are shown in Fig. 3. The lower scaling exponent ($\nu \sim 0.65$) on the left panel indicates weaker LRTC and is associated with rather quickly changing and shorter periods of elevated activity in the amplitude fluctuations of alpha oscillations (Fig. 3 [B] left panel). In contrast, stronger LRTC (indicated by $\nu \sim 0.78$) on the right panel are characterized by typical intermittent fluctuations of the amplitude at different timescales (Fig. 3 [B] right panel), which are indicative for pronounced LRTC.

3.3. Alpha power at rest and cognitive performance

3.3.1. California Verbal Learning Test-II: attention span

Sensor space. Alpha power at rest positively correlated with the number of words successfully recalled after the first presentation of each CVLT-II list (list A and list B), reflected in the attention-span score. The findings in sensor space revealed bilaterally widespread positive correlations, which were significant according to cluster statistics with $p = 0.012$ (Fig. 4 [A]). The relationship between both measures was strongest at the Fz electrode ($p < 0.007$, $\rho = 0.3$; Fig. 4 [B]).

Source space. Source space analysis showed that the most significant correlations were located primarily in the left- and to a smaller extent also in the right-hemisphere (two clusters were significant with $p = 0.02$ and $p = 0.035$ after permutation testing, see Fig. 4 [C]). The strongest correlations, based on the region of interest (ROI) analysis, were observed at the left anterior cingulate cortex (ACC), left supplementary motor cortex (SMA), left postcentral gyrus (IPoCG), left superior parietal lobule (SPL) and right SMA extending to the right ACC to a weaker extent.

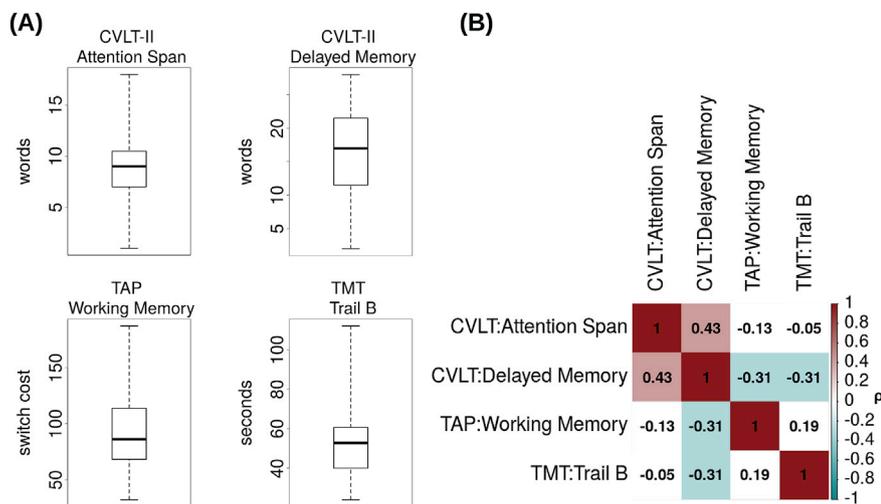


Fig. 1. Task performance in different cognitive tests and correlation matrix of test scores. Only moderate to weak correlations were detected between different test scores. (A) The boxplots display the median marked as a bold line and 50% of the scores. The lower and upper whiskers represent another 50% of scores distributed outside the interquartile box. (B) Correlation matrix of Spearman's rank correlation coefficients (ρ), where significant correlations ($p < 0.05$) are color-marked. Abb.: TAP - Test for Attentional Performance; TMT- Trail Making Test; CVLT-II - California Verbal Learning Test.

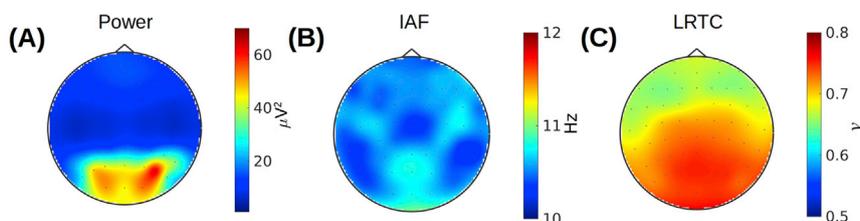


Fig. 2. Grand-average topographic maps of alpha band measures (8–12 Hz) in EEG sensor space. (A) Alpha power; (B) IAF; (C) LRTC. Abb.: IAF- individual alpha peak frequency; LRTC - long-range temporal correlations.

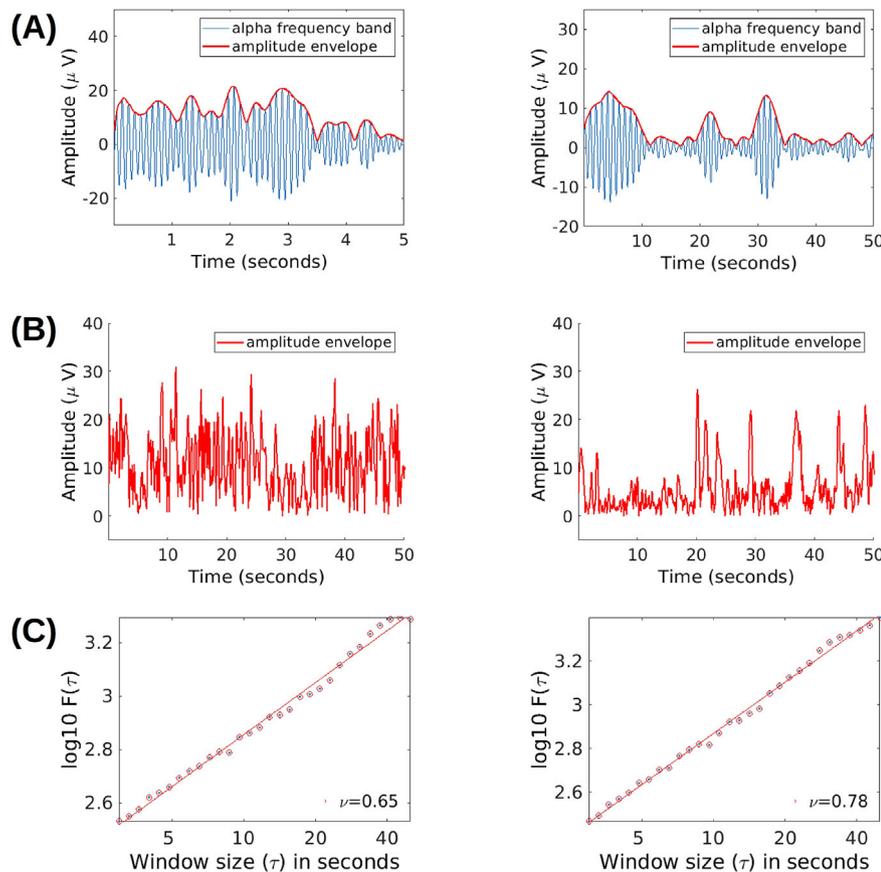


Fig. 3. Two examples of LRTC in the amplitude envelope of resting state alpha oscillations (8–12 Hz) in sensor space. The data from the P2 electrode of two representative participants show subject-specific amplitude dynamics. The left column (panels [A] to [C]) displays data of a participant with relatively low LRTC ($\nu \sim 0.65$), the right column depicts a participant with a comparatively high scaling exponent ($\nu \sim 0.78$). (A) Five seconds of band-pass filtered EEG between 8 and 12 Hz and its amplitude envelope marked in red. (B) The amplitude envelope of alpha oscillations is displayed across 50 s, and figure below (C) depicts its fluctuation $F(\tau)$ as a function of window size τ , as analyzed by using DFA. Here, the scaling exponent (ν) indicates the slope of the least-squares line. Abb.: DFA - detrended fluctuation analysis; LRTC - long-range temporal correlations.

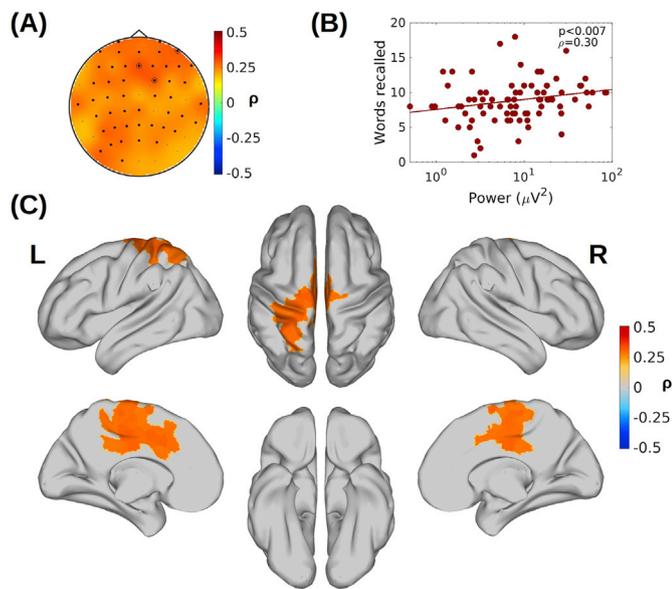


Fig. 4. Spearman correlation shows a significant relationship between attention-span scores and resting-state power in alpha oscillations (8–12 Hz). (A) Sensor space results indicated that higher alpha power at rest was associated with increased attention-span (CVLT-II) score. Significant correlations at $p < 0.05$ are marked as bold channels and are circled for $p < 0.01$. (B) Across-subjects scatter plot of the relationship between the power and the task score is shown for the electrode Fz. (C) Color-coded correlation-coefficient values at source space are plotted on the cortical surface. Source space analysis revealed the following regions with significant correlations: left and to a weaker extent right ACC, bilateral SMA, and left parietal regions (i.e., lPoCG and lSPL). Abb.: ACC - anterior cingulate cortex; CVLT-II - California Verbal Learning Test-II; L - left hemisphere; lPoCG - left postcentral gyrus; R - right hemisphere; SMA - supplementary motor area; lSPL - left superior parietal lobule.

3.3.2. Alpha power at rest and other tests

No significant correlations were found between alpha power measured at rest and test scores obtained with CVLT-II: Delayed memory, TAP: Working memory, or TMT: trail B that measured long-term memory, working memory, and executive functions, respectively.

3.4. Individual alpha peak frequency and cognitive performance

No correlations between IAF at rest and cognitive test scores were significant after correcting for multiple comparisons across tests.

3.5. Long-range temporal correlations at rest and cognitive performance

3.5.1. Test of Attentional Performance: switch-cost score

Sensor Space. Fig. 5 (A) shows the scalp topography of the correlation coefficients between scaling exponents at each sensor and the switch-cost score. Overall, these correlations were negative, thus indicating that faster and more accurate switching (i.e., lower scores) was related to higher scaling exponents measured at rest. The spatial distribution of the correlation coefficients was rather broad with maximal values above the right hemisphere. This cluster was significant at $p = 0.003$. Fig. 5 (B) shows a scatterplot for switch-cost scores and scaling exponents measured at channel FC2 ($p < 0.001$; $\rho = -0.45$) across all participants.

Source space. Similar to the sensor space, results in source space also revealed a widespread correlation-coefficient distribution with the right-hemispheric lateralization. Three clusters stayed significant after permutation tests with p-values in the range between 0.0009 and 0.017 (Fig. 5 [C]). The strongest correlations were present at regions in the right superior frontal and precentral gyrus (rSFG and rPreCG), right

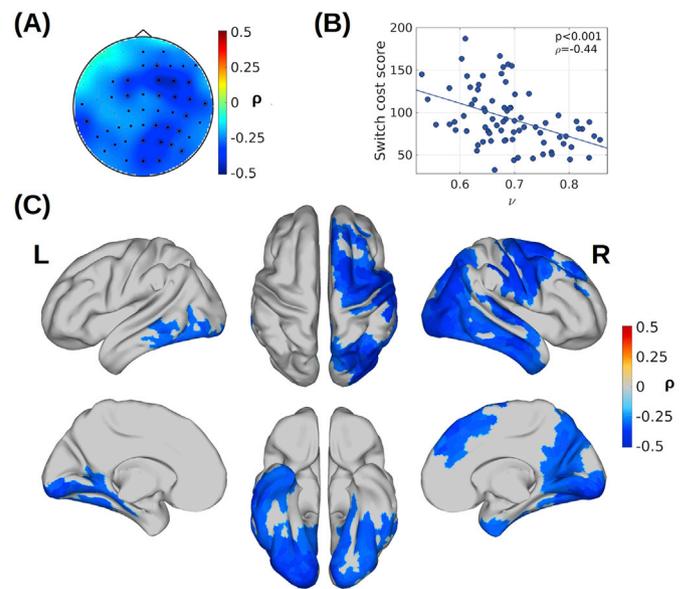


Fig. 5. Spearman correlation shows a significant relationship between working memory performance and LRTC in resting-state alpha oscillations (8–12 Hz). (A) Negative correlations in sensor space indicated that higher scaling exponents related to lower switch-cost score indicating more accurate and faster working memory performance. Significant correlations at $p < 0.05$ are marked as bold channels and are circled for $p < 0.01$. (B) Scatter plot across subjects of the most significant correlation at the electrode FC2. (C) Results at source space showed that the strongest correlations were in the right hemisphere, namely in right frontal (e.g., rSFG), temporal (e.g., rTG), parietal (e.g., rSMG), and right and left occipital (e.g., rLOC and lLING) regions. Abb.: lLING - left lingual gyrus; LRTC - long-range temporal correlations; rLOC - right lateral occipital cortex; rPreCG - right precentral gyrus; rSFG - right superior frontal gyrus; rTG - right temporal gyrus; rSMG - right supramarginal gyrus; TAP - Test for Attentional Performance.

supramarginal gyrus (rSMG), right temporal gyrus (rTG), multiple areas in the right lateral occipital cortex (rLOC) and left lingual gyrus (lLING).

3.5.2. Long-range temporal correlations at rest and other tests

No significant correlations were found between scaling exponents and CVLT-II subtests measuring verbal memory, or TMT: trail B suggested to reflect performance of executive functions.

4. Discussion

The present study demonstrated that cognitive task performance, which involved verbal memory and working memory demands, was related to neural activity measured at rest. Specifically, (i) the number of words recalled after the first presentation of a list in a verbal memory task (measured with CVLT-II: Attention span) was positively correlated with RS alpha power; this relation was most pronounced in the left hemisphere (i.e., the anterior cingulate cortex, supplementary motor area, and parietal regions) and to a lesser extent also in the right hemisphere (e.g. supplementary motor area). Furthermore, (ii) better working memory performance (measured with the switch-cost score using TAP) was associated with increased RS-LRTC. The strongest correlations were seen in the right hemisphere, primarily in frontal, temporal, occipital, and parietal regions. In line with previous studies (e.g., Samek et al., 2016; Bazanova, 2012; Klimesch et al., 2007), our results contribute to a further understanding of the functional significance of RS neural activity in alpha frequency ranges for cognitive task performance. Moreover, our findings suggest the presence of distinct cognitive control networks at rest that possibly govern sustained and phasic attention during task performance (Sadaghiani and Kleinschmidt, 2016), which will be discussed in the following sections.

4.1. Conceptual and methodological considerations

One possible limitation of the present study design is that the cognitive testing and RS-EEG recordings were performed on different days. However, previous studies showed stability across recording sessions and even heritability of alpha-band measures (Smit et al., 2005; Linkenkaer-Hansen et al., 2007; Nikulin & Brismar, 2004), which in turn implies that neuronal properties measured at one day should relate to cognitive testing on a different day.

Complementing previous work that related oscillatory measures to task performance, we investigated alpha power, IAF, and LRTC measures, which allowed us to differentiate distinct “static” (power, IAF) and “dynamic” (LRTC) measures of neuronal activity to task performance. To the best of our knowledge, this is the first attempt to investigate these complementary measures of alpha oscillations in one study and examine their relation to higher order cognitive task performance involving domain-general and task-specific components. Notably, by using several tasks, we controlled for task heterogeneity (see Oswald et al., 2017; Fagerholm et al., 2015) employing modality- (auditory, visual) and domain-specific (verbal, numeric) stimuli. Importantly, domain-general components can be assessed on the basis of (i) behavioral performance (e.g., Friedman and Miyake, 2017; Wilhelm et al., 2013) and (ii) topographically similar activations of neuronal networks involved in cognitive control (Sadaghiani and Kleinschmidt, 2016; Dosenbach et al., 2007; Gazzaley & D’Esposito, 2006; Miyake et al., 2000). While we demonstrated results supporting domain-generality in the neurophysiological domain, we did not find a strong evidence for it as seen from behavioral findings (cf. Fig. 1 [B]). One possible explanation could be the selection of tests and also the involvement of lower-level, modality-specific components, which are separable from the domain-general executive processes and which allow for different strategies that could possibly influence test results (Friedman and Miyake, 2017; Lorenz et al., 2017). While a hypothesized domain-general factor could not be extracted in the current study based on behavioral test scores, future studies might investigate this relation by employing a larger set of tasks, which might increase the chances to detect domain-general components.

4.2. Individual alpha peak frequency (IAF) at rest does not relate to cognitive task performance

We did not find significant correlations between IAF and performance in any of the tasks. Indeed, previous findings on this subject remain heterogeneous: While several studies reported increased (~1 Hz) IAF in better performers compared to poor performers especially in tasks associated with intelligence and memory demands (Grandy et al., 2013; Clark et al., 2004; Klimesch et al., 1997), these results, however, were not replicated by other researchers (e.g. Angelakis et al., 2004; Posthuma et al., 2001). In general, the absence of a significant relation between IAF and cognitive performance might reflect the fact that the task performance might be modulated by other mechanisms not necessarily reflected in oscillatory peak frequency.

4.3. Alpha power at rest relates to attention-span score

The present study revealed that alpha power at rest positively correlated with the number of words recalled after the first presentation of a list (cf. Fig. 4) — a task that requires encoding and maintenance of information at the time of its presentation (DeJong and Donders, 2009; Donders, 2008). In principle, such encoding trials (i.e., encoding all sequentially presented words of the list) could be differentiated from the subsequent updating trials, that is, when the recalled list of words is updated with new words and learned after each consequent repetition (DeJong and Donders, 2009). Moreover, the functional significance of alpha power was previously related to encoding trials in the inhibition-timing hypothesis: Alpha power was suggested to reflect top-down attention control that allows focusing on task performance

especially during encoding and retention (Klimesch et al., 2007), likely reflecting sustained attention - the ability to maintain alertness over time when information is being encoded (Jongman et al., 2015). In terms of the attention-span task, sustaining incoming information that is being encoded is of pivotal importance, since verbal stimuli is expected to be maintained until the time of recall. The present finding complements previous studies relating RS alpha power to memory performance (Prat et al., 2016; Klimesch, 1999; Vogt et al., 1998).

Given these findings, our hypothesis was partially confirmed: Although the power of alpha oscillations at rest correlated with domain-general aspects of cognitive performance (i.e., sustained attention as discussed further) on the neurophysiological level, the most significant regions were not situated at the fronto-parietal (FP) network but instead extended to the anterior cingulate cortex and neighbouring regions. These regions overlap to a bigger extent with the cingulo-opercular (CO) network - one of the networks associated with cognitive control, previously described by Dosenbach et al. (2007). The CO network was suggested to be involved in a stable task-set maintenance, which relies on sustained attention (Sadaghiani and Kleinschmidt, 2016; Dosenbach et al., 2007) and domain-general information encoding (Li et al., 2014; Fletcher et al., 1995), consequently found in our study. Moreover, it is important to note that the most significant regions were to a larger degree extended to the left hemisphere, which is in line with previous findings of left-hemispheric involvement during verbal information processing and its output (including left parietal regions; Brownsett and Wise, 2010), attention, and cognitive control (Botvinick et al., 2004). The involvement of the left and right SMA could be linked to an inhibitory control of a preparatory motor response of speech production (Wardak, 2011; Alario et al., 2006; Heun et al., 2000). Notably, these findings suggested a possible involvement of not only domain-general but also domain-specific components, associated with verbal stimuli processing. To summarize, the present results suggest the relevance of alpha power at rest for tasks that require sustained attention and prolonged encoding of incoming information.

4.4. Long-range temporal correlations at rest relate to working memory performance

While previous studies on LRTC reported their relation to the performance of perceptual (Palva et al., 2013), motor (Smit et al., 2013), and decision-making (Colosio et al., 2017) tasks, the present findings revealed a relation between LRTC in the amplitude envelope of alpha oscillations and higher-order cognitive performance. Specifically, our findings demonstrated a strong correlation between working memory performance and LRTC up to 50 s: Increased LRTC at rest corresponded to better switching capacity (measured with the switch-cost score) in the n -back task (cf. Fig. 5).

Previous studies have reported that LRTC characterize neuronal network activity near a critical state (Poil et al., 2012; Linkenkaer-Hansen et al., 2001) that is likely to be optimal for information transmission and memory formation (Shew and Plenz, 2013; Shew et al., 2011; Beggs and Plenz, 2004). Importantly, it has been shown in a computational study (Poil et al., 2012) that stronger LRTC in neuronal oscillations may relate to an optimal balance between excitation and inhibition. Such a balance of neuronal activity might enable stability (maintaining information) and modulation (information updating) that is congruent with working memory task demands (Eriksson et al., 2015), also shown in the present study.

Consequently, we suggest that increased LRTC at rest might indicate the presence of neuronal resources that relate to efficient and fast information processing in neuronal networks suggested to be relevant for task performance. Accordingly, we found that the negative correlation between LRTC and the switch-cost score (indicating that higher LRTC relate to faster and more accurate switching) was maximal for right-hemispheric frontal, temporal, occipital, and parietal regions. This result is in line with our hypothesis and previous studies suggesting that FP networks are involved in a variety of tasks that require phasic adaptive

cognitive control (Eriksson et al., 2015; Zanto and Gazzaley, 2013; Dosenbach et al., 2007; Sauseng et al., 2005). Importantly, regions that were found to account for cognitive control in working memory tasks highly overlap with the regions found in the present study: the prefrontal cortex (i.e., middle frontal gyrus near the precentral sulcus, right inferior frontal junction) and parietal regions (e.g., the right intraparietal sulcus; Gazzaley and Nobre, 2012; Bollinger et al., 2010; Gazzaley & D'Esposito, 2006). Specifically, frontal and fronto-parietal regions were suggested to facilitate flexible and goal-directed behavior by inhibition (Aron et al., 2014), especially when task requirements include switching (Dodds et al., 2011) and novelty aspects (Corbetta and Shulman, 2002). It is important to note that *n*-back tasks involve processing of not only novel (incongruent trials), but also familiar (congruent trials) numeric stimuli (Stern et al., 2001), which were previously linked to the involvement of temporal and occipital regions, thus supporting long-lasting representations (Hasselmo and Stern, 2006; Stern et al., 2001) through long-term memory demands (Unsworth and Engle, 2007), consequently found in the present study. To summarize, our findings revealed the presence of LRTC at rest in regions that involve not only domain-general cognitive control (i.e. phasic adaptive control), but also regions that support task-specific demands.

4.5. Long-range temporal correlations and Trail Making Test: differences in task sampling rates

Despite the observed correlation between LRTC and switching capacity in the TAP working memory task, no correlations were found between LRTC and the TMT trail B, which is also thought to employ working memory components (Sánchez-Cubillo et al., 2009). We suggest that these findings may be due to different timescales in which the scores are obtained: While the TAP test scores are derived after each button press, thus having millisecond precision and capturing the fluctuating output of cognitive operations with a relatively high sampling rate, the TMT trail B test performance is characterized by a single score obtained after completing the task, here by approximately 40–60 s (cf. Fig. 1 [A]). Interestingly, LRTC, which can be described as a comparatively “dynamic” measure of neural oscillations (see Fig. 6), correlated only with

the former working memory score that was obtained with higher temporal precision. To conclude, the present findings suggest that in order to relate brain activity measures to cognitive performance, not only should cognitive constructs presumably associated with the respective test be considered, but also the sampling frequency of cognitive–motor operations.

4.6. Cognitive control networks: interpretation of the functional role of alpha power and LRTC at rest

An overarching scheme integrating all our results is provided in Fig. 6. The topography of correlations between measures of alpha oscillations and task scores in our study is consistent with the dual-network model proposed by Dosenbach et al. (2007). According to this model, the CO and FP networks are characterized by differential functional connectivity patterns which are similar at rest as well as task conditions. These networks reflect different cognitive control functions during the task performance: The CO network operates on a stable set maintenance and sustained attention, whilst the FP network supports phasic adaptive control (Sadaghiani and Kleinschmidt, 2016; Dosenbach et al., 2007).

Sadaghiani and Kleinschmidt (2016) complemented this model by suggesting the importance of cognitive control networks for generating alpha oscillations in order to enable task-control. The CO network was hypothesized to modulate rather widespread oscillatory alpha power increase and noise cancellation, thus enabling sustained attention and downstream cognitive control once task demands are met. In line with these notions, our present results indicate the importance of RS alpha power, defined as a ‘static’ measure, in the dorsal anterior cingulate cortex and neighbouring regions for sustained attention in a verbal memory task (i.e., CVLT-II). Importantly, it was possible to differentiate this network from the FP network that is thought to govern phasic adaptive control by distant network communication through long-range alpha phase locking (Sadaghiani and Kleinschmidt, 2016). Because we have demonstrated that LRTC in the amplitude of alpha oscillations during rest in the FP network relate to working memory (through switching capacity that requires fast updating of information), we propose that LRTC, defined as a ‘dynamic’ measure, might consequently enable phasic control realised through quick adaptation to changing task demands (Posner, 2008). Interestingly, and in line with our results, the FP network was also found to operate on different timescales and was suggested to adjust the control on trial-by-trial bases and error-related activity (Dosenbach et al., 2007) for which LRTC at neuronal networks might be beneficial.

Our findings could be summarized on the basis of topographical and behavioral results. Topographies of RS alpha power and LRTC, that were linked to cognitive performance, had considerable overlap with CO and FP networks respectively, which is consistent with the dual-network model (Dosenbach et al., 2007). Taking into account phasic and sustained aspects of the cognitive tests, our results thus suggest a rather multifaceted than a unitary view of a domain-general cognitive control.

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	TAP: Working Memory	CVLT-II: Attention Span
Task features		
Cognitive control Stimuli	Phasic Numeric	Sustained Verbal
Topographic findings		
Measure Property	LRTC at α oscillations “Dynamic” measure	Power of α oscillations “Static” measure
Domain-general Domain-specific	Right Fronto-Parietal Right temporal, occipital	Left Anterior Cingulate Cortex Left and right SMA
		

Fig. 6. Summary of present results depicted schematically. The findings reveal significant relations between cognitive task performance and oscillatory alpha activity at rest in two major cognitive control networks, namely the fronto-parietal and anterior cingulate cortex, including neighbouring regions. These domain-general networks have been previously considered to relate to aspects of task performance, accounting for different cognitive control functions governing phasic and sustained attention, respectively. Furthermore, relations with cognitive task performance were also observed in temporal, parietal, and occipital regions, which could possibly be associated with domain- and task-specific demands. Abb.: CVLT-II - California Verbal Learning Test; LRTC - long-range temporal correlations; TAP - Test of Attentional Performance.

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