Modulation of aperiodic EEG activity provides sensitive index of cognitive state changes during working memory task

Tisa Frelih [1,2,3,*], **Andraž Matkovič** [3,4,*], **Tjaša Mlinarič** [3,5], **Jurij Bon** [1,2,3], **and Grega Repovš** [4]

[1]University Psychiatric Clinic Ljubljana, Slovenia; [2]Faculty of Medicine, University of Ljubljana, Slovenia; [3]Department of Neurology, University Medical Centre Ljubljana, Ljubljana, Slovenia; [4]Department of Psychology, Faculty of Arts, University of Ljubljana, Ljubljana, Slovenia; [5]Department of Neuroscience, Laboratory for Neuro- and Psychophysiology, KU Leuven, Leuven, Belgium; [*]These authors contributed equally to this work and share first authorship.

To better understand cognitive processes, it is essential to examine the interplay between periodic (oscillatory) and aperiodic electrophysiological brain activity. In this study, we aim to clarify how the periodic and aperiodic electrophysiological components respectively reflect the cognitive processes involved in working memory. Fifty-seven participants performed an n-back task while their brain activity was recorded using EEG. The analysis of both components of the EEG spectrum during task performance indicate that both periodic and aperiodic activities exhibit distinct task-related spatiotemporal dynamics that are closely related to cognitive demands. The results indicate that the substantial changes traditionally attributed to theta oscillations in working memory tasks are, in fact, due to shifts in the spectral slope of aperiodic activity. This suggests that the modulation of aperiodic activity associated with cognitive control processes may provide a more sensitive index of cognitive state changes than previously recognised. Our findings challenge the conventional understanding of theta oscillations in cognitive processing and question the routine practice of EEG baseline correction in time-frequency analysis, which may obscure significant modulations in continuous working memory tasks. Consequently, the inclusion of aperiodic activity as a fundamental component of EEG analysis is critical to the accurate representation of the neural basis of cognition.

aperiodic activity | theta oscillations | working memory | n-back | EEG analysis

Correspondence: ***andraz.matkovic@ff.uni-lj.si***

Introduction

Working memory is a crucial cognitive ability that enables goal-directed behaviour and higher cognitive function. It involves the ability to maintain and manipulate information in the absence of sensory stimuli in support of an ongoing task (Baddeley, 2012) and is dependent on a complex set of cognitive processes and neural mechanisms (Wager and Smith, 2003). Due to its core role in cognition, working memory has been an object of intense research interest in cognitive neuroscience including electroencephalography (EEG). This method allows for time-frequency analysis of brain activity (Cohen, 2014), which typically focuses on changes within predefined frequency bands. One frequently used experimental paradigm for studying working memory mechanisms using time-frequency analysis is the n-back task (Figure 1). This task integrates key working memory processes such as encoding, maintenance, updating, and recall of stored information (Owen et al., 2005; Gevins et al., 1997). Power spectra dynamics in this ongoing working memory task are typically attributed to oscillatory activity (Coleman et al., 2023; Pesonen et al., 2007; Chen and Huang, 2016). Theta oscillations (4–8 Hz) are often shown to play a significant role in cognitive control and working memory processing (Palomäki et al., 2012; Scharinger et al., 2017; Pesonen et al., 2007), while event-related responses in the alpha (6–12 Hz) and beta (13–30 Hz) range have been linked to attention and other cognitive processes, related to working memory (Krause et al., 2010; Gevins et al., 1997; Coleman et al., 2023).

EEG power spectra are characterised by $1/f$ power scaling, i.e. power decreases as frequency increases, introducing the aperiodic component into the analytical framework. This component complicates interpretation of the results by potentially obscuring changes in periodic (oscillatory) activity, as it represents a continuous spectrum of activity that does not conform to discrete oscillatory patterns (Cohen, 2014; Donoghue et al., 2020b). To overcome this challenge and to improve the clarity of task-related changes in time-frequency analysis, baseline correction is often used.

Baseline correction aims to normalise the data by subtracting the aperiodic background in order to isolate and examine the oscillatory dynamics more clearly. However, there are two main problems with the use of baseline correction. First, the n-back task requires continuous cognitive processes such as information maintenance during inter-trial-interval, most commonly used to estimate baseline activity, resulting in no neutral (pre-stimulus) baseline activity to which to compare stimulus-related processing and responses. Second, the use of baseline correction methods (implicitly) assumes that aperiodic activity remains stable over time and is dismissed as background noise (Gyurkovics et al., 2021;

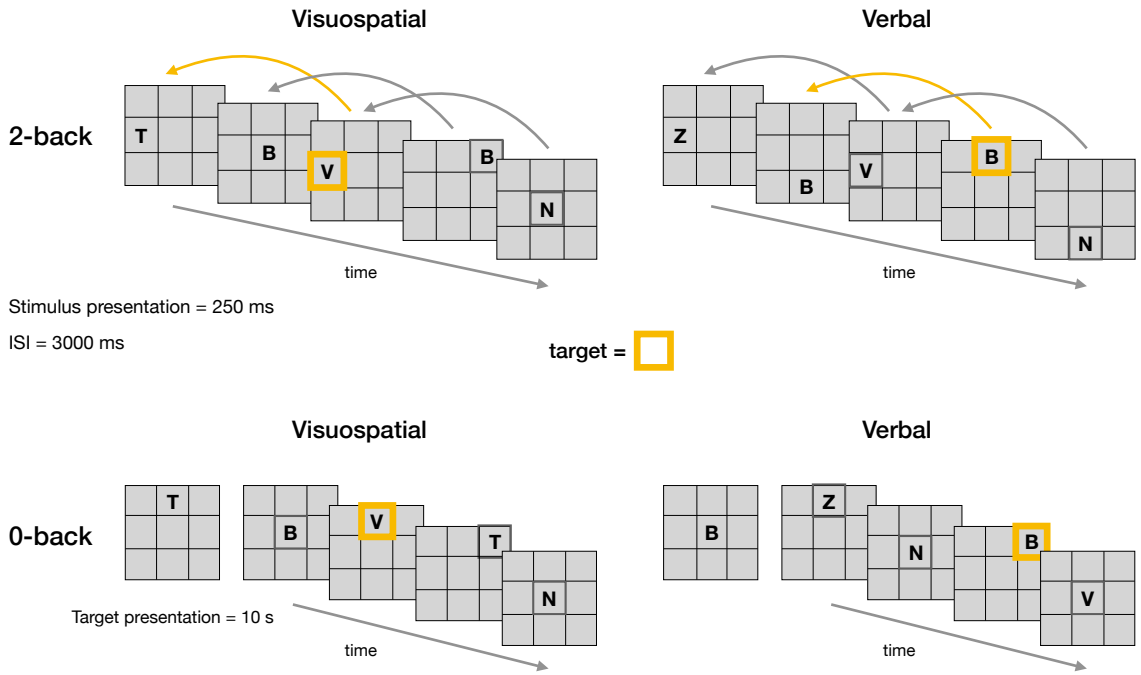

Figure 1. Schematic representation of the n-back task.
The n-back working memory task was conducted in two distinct modalities: visuospatial and verbal. In the 2-back condition, participants had to identify whether the current stimulus matched the one presented two steps previously. In the visuospatial modality, the target was a spatial location, whereas in the verbal modality, the target was a letter. In the 0-back condition participants' task was to respond to a predefined target, with the type of target corresponding to the task modality. Target stimuli are highlighted in orange.

Merkin et al., 2023; Donoghue et al., 2020b), and therefore its dynamics are not taken into account.

Recent studies investigating task-related fluctuations in aperiodic activity (Gyurkovics et al., 2022; Virtue-Griffiths et al., 2022; Akbarian et al., 2023; Kałamała et al., 2024) have shown that ignoring these dynamics can distort oscillatory measurements and obscure important physiological and behavioural information (Gyurkovics et al., 2021; Donoghue et al., 2020a). Thus, subtracting baseline activity removes important information, whereas not doing so makes it difficult to observe significant task-related changes. Our aim is to reassess previous interpretations obtained through conventional EEG analysis methods by investigating the respective contributions of aperiodic and periodic (oscillatory) activity to the overall power spectrum dynamics (Figure 2) during the n-back task, without losing important information that baseline correction might introduce.

The common approach to time-frequency analysis assumes that the observed peaks in the measured power spectrum mainly reflect modulations of periodic activity. In fact, the presence of power in a particular frequency band is not necessarily indicative of oscillatory dynamics, as aperiodic activity can make up a significant proportion of the observed power spectra (Bullock et al., 2003; Donoghue et al., 2020a, 2022). Computational modelling has suggested that the aperiodic activity measured by EEG reflects the balance between excitation and inhibition (E:I) of the brain (Gao et al., 2017; Lim and Goldman, 2013), which is essential for efficient cognitive processes (Ahmad et al., 2022). Aperiodic activity spans the entire frequency range, varies continuously, and can be described by a linear slope when plotted in semi-logarithmic space (Donoghue et al., 2020b; He, 2014). A steeper slope indicates higher power at low frequencies, often associated with more intense cognitive processing, while a flatter slope signals more even power distribution across frequencies (Gyurkovics et al., 2022; Kałamała et al., 2024), possibly indicating a less engaged brain, weaker E:I balance and lower cognitive performance, including working memory (Akbarian et al., 2023; Kałamała et al., 2024; Lendner et al., 2023). Variations in aperiodic slope have been found to be modulated by age (Voytek et al., 2015; Dave et al., 2018; Merkin et al., 2023) and mental state (Donoghue et al., 2020a; Podvalny et al., 2015; Waschke et al., 2021). Moreover, task-related changes in overall power, typically interpreted as oscillatory dynamics, may be significantly co-modulated by the aperiodic slope shift (Akbarian et al., 2023; Gyurkovics et al., 2022; Virtue-Griffiths et al., 2022) Given these recent demonstrations of the functional role of aperiodic activity and its dynamics, it's methodologically imperative to carefully parameterise both periodic and aperiodic spectral features of an EEG before interpreting time-frequency analysis results.

In this study, we aim to explore the distinct role of the aperiodic component in the n-back task and investigate possible differences between aperiodic and peri-

odic components in relation to the cognitive demands of the task. This focus on the aperiodic component offers a novel perspective on working memory mechanisms. Furthermore, we question the influence of commonly used baseline correction methods on the measurement of oscillatory activity, which is in line with the investigation of aperiodic activity dynamics. Unaccounted-for aperiodic activity might have biased the measures of oscillatory dynamics reported in previous n-back studies, while its own dynamics were not investigated.

The study's main objective is to investigate whether the dynamics of aperiodic activity in the n-back task are influenced by memory load, stimulus type, or modality. We expect to replicate a steepening aperiodic slope after the stimulus onset, as previously reported by Akbarian et al. (2023); Gyurkovics et al. (2022); Virtue-Griffiths et al. (2022).

Our study builds on previous research by using high temporal resolution data to investigate the dynamics of the aperiodic slope in two modalities (visuospatial/verbal). Additionally, in contrast to other n-back studies that examine peristimulus intervals using discrete time windows (Akbarian et al., 2023; Kałamała et al., 2024), we analyse the activity at each time point within this range, offering a more detailed perspective. It is important not to overlook possible fluctuations in the aperiodic slope that may occur in short time periods, as they may provide valuable insights into the dynamics of aperiodic activity during the continuous working memory task.

We hypothesised that the aperiodic slope would be modulated by the processing demands of the n-back task, and that this modulation would vary according to differences in load and stimulus type. We did not expect modality-dependent differences in aperiodic activity, as the modulation of the post-stimulus slope suggests a global inhibitory response in the brain (Gyurkovics et al., 2022).

The reason for our focused examination of aperiodic activity is its potential to redefine our understanding of cognitive workload and efficiency in working memory tasks. Additionally, we aim to provide a novel perspective on the dynamic interplay between aperiodic and periodic activities during the n-back task. By distinguishing between these two types of activities, this study addresses the baseline correction problem inherent in continuous tasks and the evolving nature of aperiodic activity. Our research aims to fill a critical gap in the existing literature by dissecting the unique contributions of aperiodic and periodic activities.

Results

We analysed the EEG data from the visuospatial and verbal n-back tasks. We transformed the data into the time-frequency domain by convolving it with superlets (Moca et al., 2021). Subsequently, we applied the FOOOF (Fitting Oscillations and One-Over-F) algorithm (Donoghue et al., 2020b) to decompose the activity into periodic and aperiodic components (Figure 2).

Changes in aperiodic activity appear as theta activity in baseline corrected time-frequency plots

As the first step of our analysis, we compared periodic and aperiodic activity with baseline-corrected time-frequency activity. In the baseline-corrected time-frequency plot, we observed a decrease in alpha and beta power up to 1 second post-stimulus, while theta power increased from 0 seconds post-stimulus (Figure 3, Figure S8). Notably, when we examined periodic activity, we only observed changes in alpha and beta, and theta activity was absent, presumably because it reflected aperiodic activity rather than oscillations.

To further confirm the absence of theta in periodic activity across our sample, we examined individual power spectra (Figure S1). Despite considerable heterogeneity among participants, we observed a distinct theta peak in only two participants.

Periodic activity changes with working memory load, stimulus type and modality

Next, we examined the differences in periodic activity as a function of task conditions. We observed a decrease in the alpha and beta bands of periodic activity in the 2-back compared to the 0-back condition over the entire trial period and over the entire scalp (Figure 4, Figure 5). Furthermore, we found a greater decrease in alpha and beta power in response to targets compared to non-targets. In addition, we observed a correlation between beta power and reaction times in central channels. This correlation was positive in the early period (up to 0.5 seconds post-stimulus) and negative in the late period (1–2 seconds post-stimulus). Finally, we observed an interaction between modality and stimulus type in the time period from 0.5 to 1 second post-stimulus, reflecting a greater difference between target and non-target stimuli in the verbal task in the alpha and beta bands compared to the visuospatial task (Figure S2).

Aperiodic activity has frontal and parietal components

We analysed the aperiodic activity separately for the parameters offset and exponent (slope). We observed two distinct components (peaks) in the time course of the exponent (Figure 6). The first component peaked at around 0.3 s after stimulus onset and was most pronounced in frontal channels, whereas the second component peaked at around 0.7 s post-stimulus and was most pronounced in parietal channels. The exponent exhibited significant differences between stimulus types (Figure 7). Specifically, the exponent was larger for targets at approximately 0.3 seconds and for non-targets at approximately 0.7 seconds post-stimulus. We observed no other differences between conditions. We found associations with reaction times at approximately

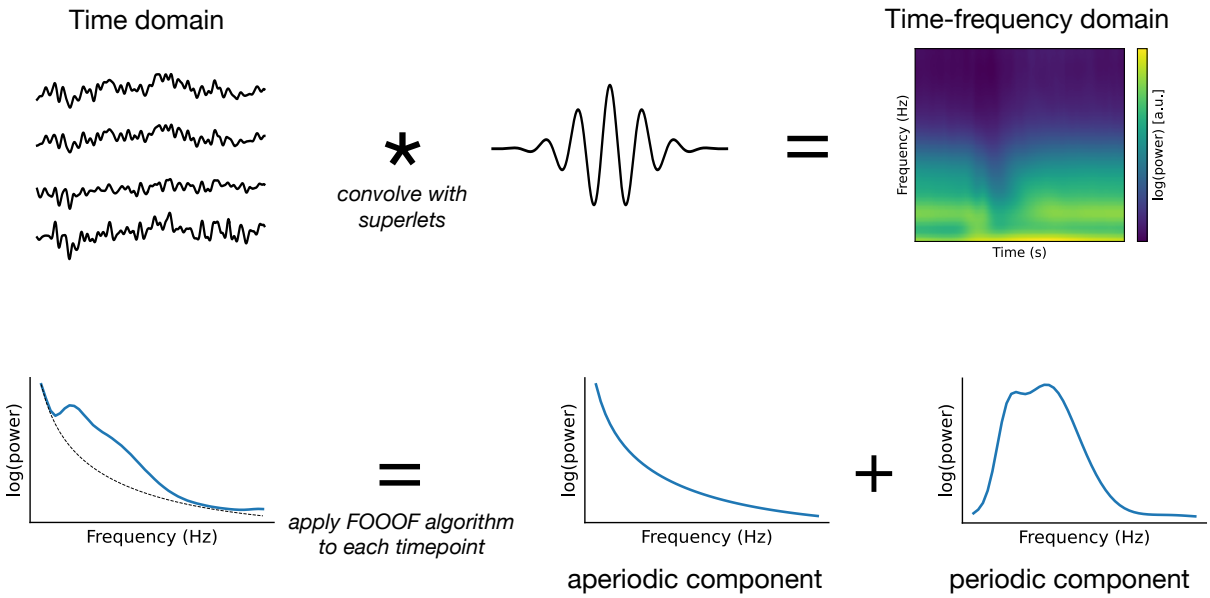

Figure 2. Schematic of the analysis.
The time domain data were first transformed into the time-frequency domain by convolution with superlets (Moca et al., 2021). Next, the periodic and aperiodic components of the power spectrum density were estimated for each time point using FOOOF (Fitting Oscillations and One-Over-F) algorithm (Donoghue et al., 2020b). The aperiodic component was further separated into the slope (exponent) and offset components.

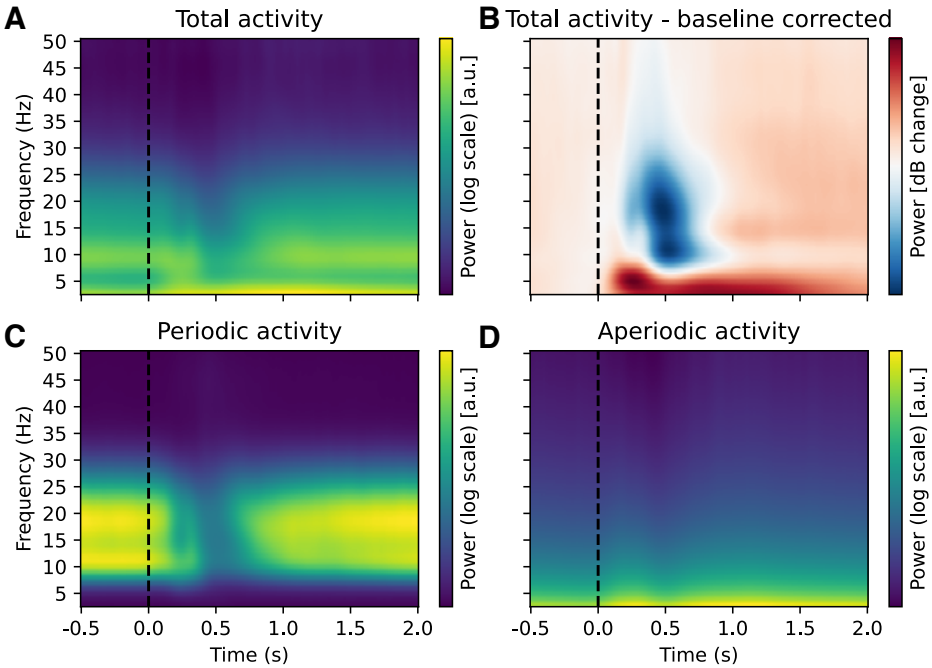

Figure 3. Effect of baseline correction and FOOOF decomposition on time-frequency decomposition.
Illustration of the effect of baseline correction and FOOOF decomposition on EEG time-frequency analysis. (**A**) "Raw" total power from time-frequency decomposition is difficult to interpret due to the $1/f$ power scaling of EEG power spectra (here representing average data across subjects, channels and conditions). In panel **B** we applied baseline correction using a pre-stimulus interval of -0.5 to -0.2 seconds for comparison. The baseline correction showed a significant decrease in alpha and beta power from 0 to 1 second and a concomitant increase in theta power lasting up to 2 seconds. However, it's unclear whether the changes in theta power are oscillatory or aperiodic. Separation into periodic (**C**) and aperiodic (**D**) components shows that changes in theta power are due to changes in aperiodic activity.

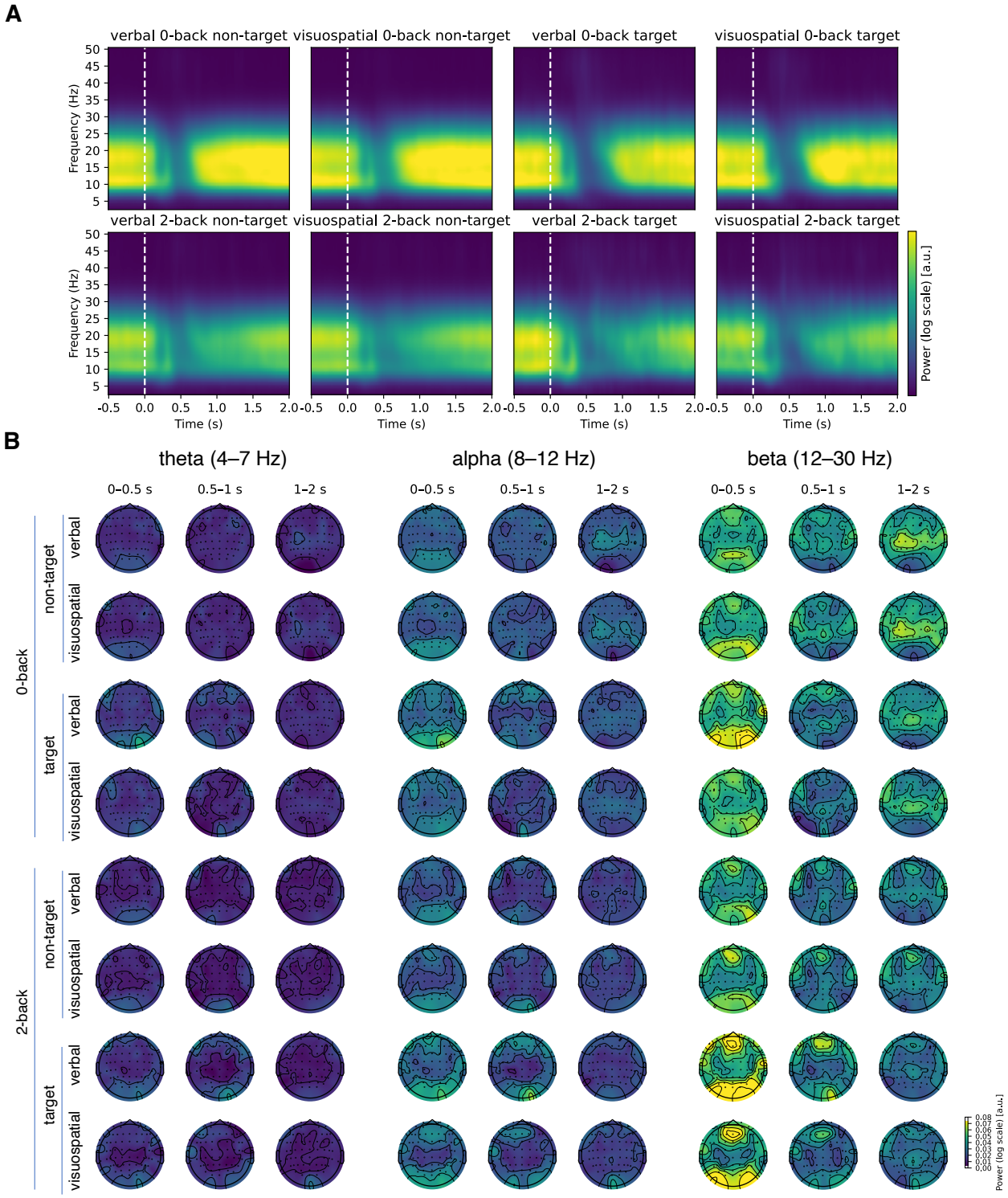

Figure 4. Changes in periodic (oscillatory) activity as a function of time.
(**A**) The inspection of periodic activity revealed strong activity in the alpha and beta frequency bands, with a sharp decrease at around 0.5 seconds post-stimulus. The power was stronger in the 0-back condition, compared to the 2-back condition (see also Figure 5). (**B**) Early beta activity was most prominent at occipital and frontal channels.

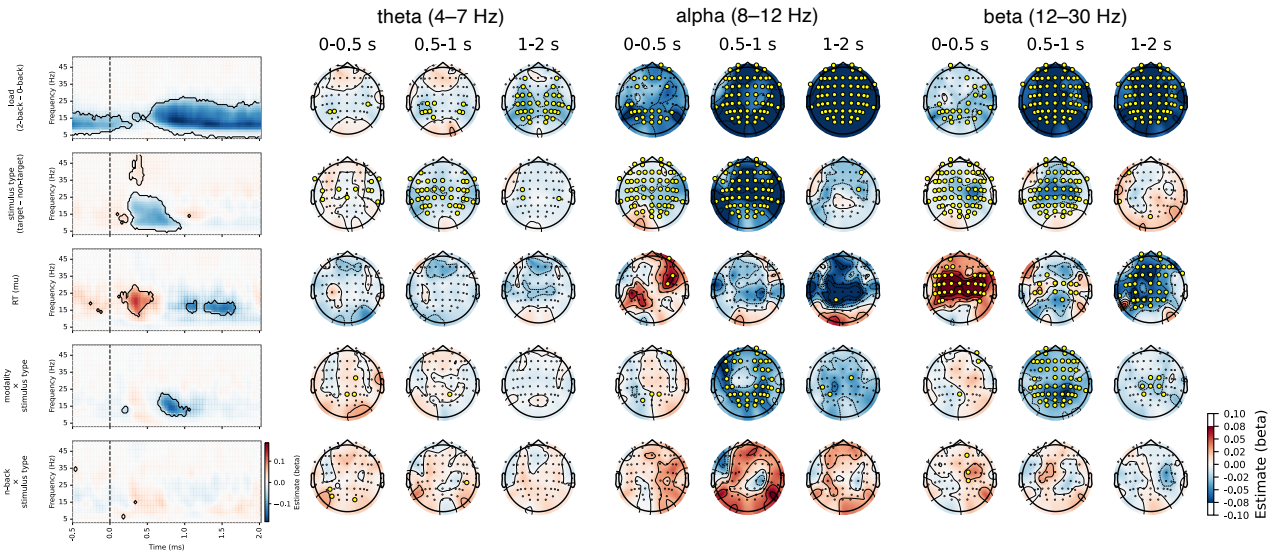

Figure 5. Results of the linear mixed model analysis of periodic activity for comparison between conditions.
Significant values are highlighted on the heatmap and marked with yellow circles on the topographies. Only factors with significant differences are shown. A p-value was interpreted as significant if it was significant in at least 3 channels or 3 time points (see Methods for details). Note that there are small discrepancies between significant values on heatmaps and topographies due to averaging across time or channels. A significant difference was observed between the 2-back and 0-back conditions, with a reduction in activity in the 2-back condition, particularly in the alpha and beta frequency bands, starting at 0.5 seconds post-stimulus. The differences between stimulus types were most evident from 0.3 to 1 second post-stimulus, with decreased activity for targets compared to non-targets across the whole scalp. Additionally, a smaller effect of the modality × stimulus type interaction was observed from 0.6 to 1 second post-stimulus (see also Figure S2 for detailed visualisation of the interaction). Associations with reaction times were significant in the beta band across central channels. These associations exhibited a positive correlation in the early phase (0 to 0.5 seconds) and a negative correlation in the later phase (1 to 1.5 seconds).

1.4 seconds post-stimulus in the parieto-occipital channels.

Similar to the exponent, offset also showed a pattern of activity with two components (see Figure S3). In addition, offset was sensitive to differences in load (lower offset for 2-back), and there was also an interaction between load × and stimulus type (see Figure S4).

Aperiodic activity does not reflect event-related potentials

To ensure that the aperiodic activity identified in our study did not simply reflect event-related potentials (ERPs), we systematically removed evoked activity from the data prior to conducting the time-frequency analysis. We then performed a correlation analysis between the topographies of ERPs and aperiodic activity for each time point, condition, and participant. We found the correlation between ERPs and aperiodic activity to be consistently low, with a value of approximately 0.25 or lower (see Figure S6 and Figure S7). This was observed throughout the entire time period examined.

Control analysis confirms main findings

To ensure the generalisability of the findings, we repeated all analyses on a publicly available dataset from a previously published study (Nakuci et al., 2023), in which participants performed a verbal n-back task with three load levels (0-, 1-, 2-back). We replicated the main findings reported above, namely the task-related modulation of alpha and beta periodic activity, and the task-related changes in aperiodic activity, which were again separated into frontal and parietal components.

Specifically, in baseline-corrected data we observed a significant decrease in alpha and beta power in the time period from 0 to 1 second post-stimulus, accompanied by an increase in theta power from 0.2 to 1.5 seconds (Figure S8). However, theta oscillations were only detected in two participants (Figure S9). The separation of EEG components revealed that while alpha and beta frequencies exhibited oscillations, theta did not. Furthermore, we observed pronounced periodic alpha/low beta activity in the frontal channels (Figure S10), which was reduced in the 2-back condition and varied with stimulus type, exhibiting increased power for non-targets. The control analysis also revealed two aperiodic components, frontal and parietal. However, these were less distinct than those observed in our data set (Figure S12, Figure S14) with the exponent associated only with cognitive load, showing higher values in the 2-back condition. Furthermore, the parietal component's exponent was found to be related to reaction times from one second post-stimulus onwards (Figure S13).

Discussion

This study provides a detailed analysis of the relationship between periodic and aperiodic neural activity during the n-back task. EEG data recorded from 57 participants performing both 0-back and 2-back tasks in visuospatial and verbal modalities were analysed to distinguish these two components within the EEG frequency spectrum. The analysis shows the presence of periodic activity in the alpha/beta frequency range prior to stimu-

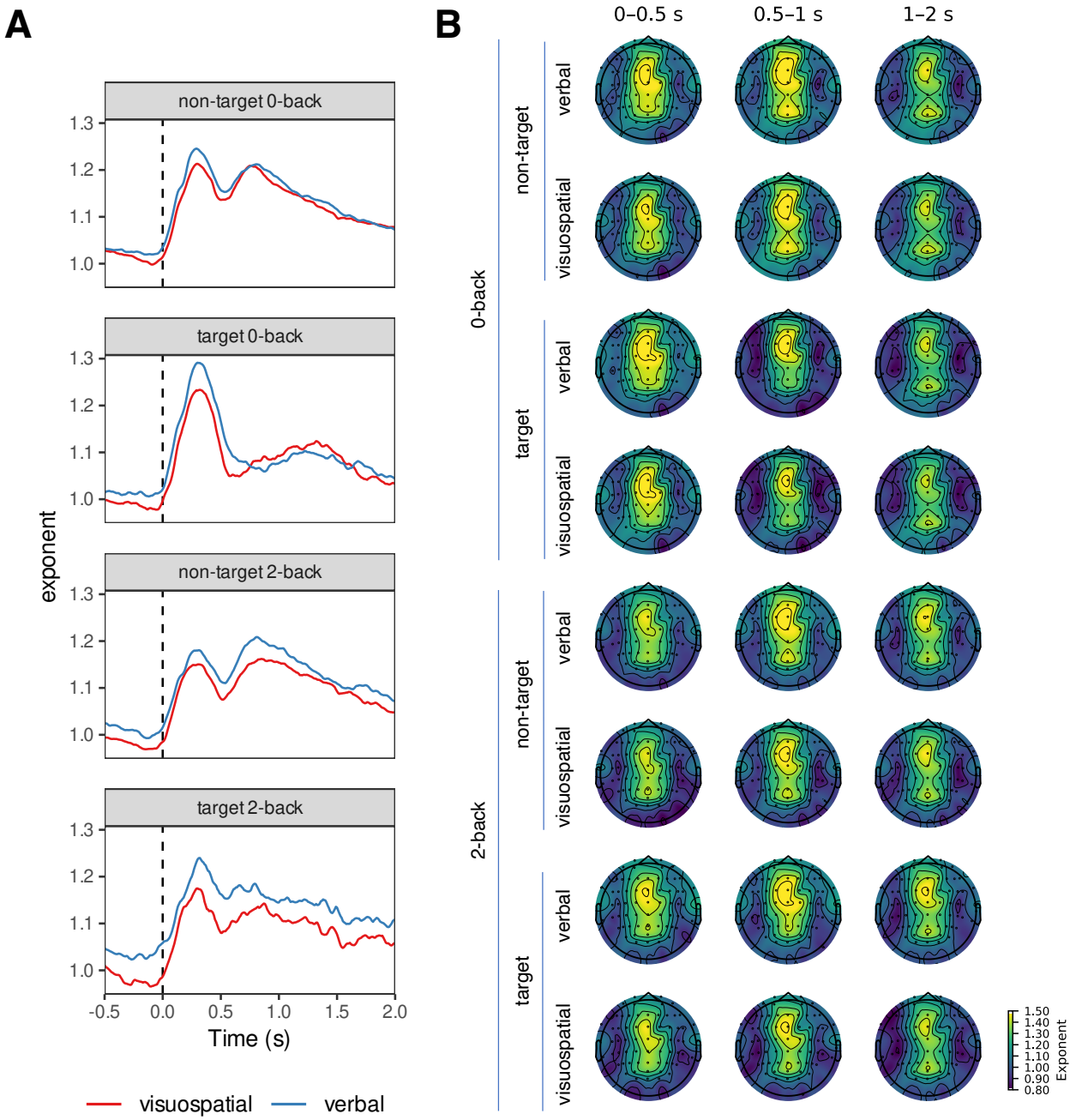

Figure 6. Changes in aperiodic activity (slope or exponent) as a function of time.
(**A**) We averaged the time course of the aperiodic activity (exponent) over all channels and observed two components (peaks) of the aperiodic activity. The first component peaked around 0.3 s post-stimulus in the frontal channels. The second component peaked at 0.7 s, was stronger in parietal channels and differed between non-target and target conditions (see Figure 7). The time course of the offset parameter was comparable, although the separation between the frontal and parietal components was more pronounced (see Figure S3).

lus onset, which modulates according to task demands. Furthermore, our results show that theta activity appears to be largely a consequence of the effect of baseline correction on aperiodic activity, which also exhibits its own task-related dynamics. This insight is crucial for the interpretation of EEG results, especially for continuous tasks such as the n-back, which require sustained working memory engagement. In addition to the interplay between the periodic and aperiodic EEG activity, the study expands on the findings of stimulus-induced spectral slope shift by identifying two neural components within the aperiodic activity. These aperiodic components are distinguished by their frontal and posterior topographic locations. Additionally, we observed task-dependent differences, including a slightly different slope modulation in non-target compared to target trials. However, we did not find any differences between modalities. Collectively, these findings enhance our understanding of the neural dynamics involved in cognitive processes during a continuous working memory task.

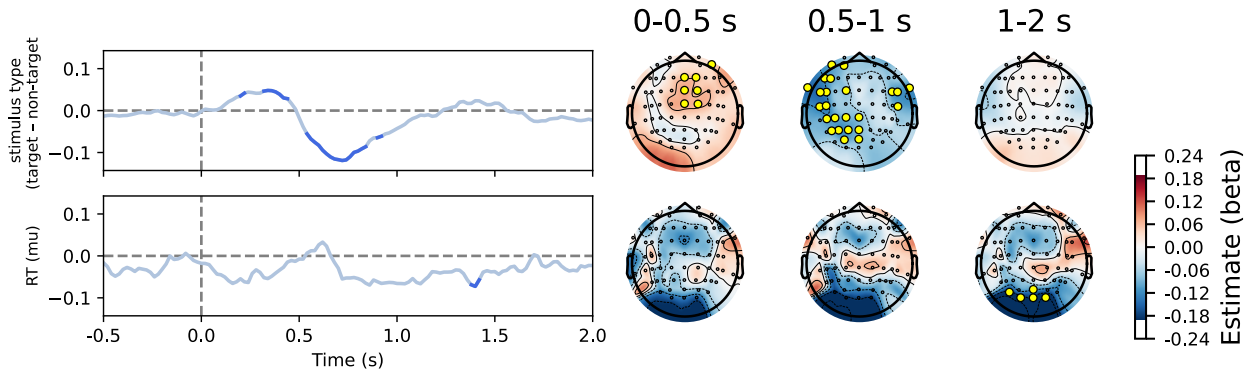

Figure 7. Results of the linear mixed model analysis of aperiodic (exponent) activity for comparison between conditions.
Significant values are shown in blue on line plots and marked with yellow circles on topographies. Only factors with significant differences are shown. The only significant differences between conditions were observed between target and non-target conditions, where the exponent was higher for targets in the early phase (0 to 0.5 s post-stimulus) and for non-targets in the middle phase (0.5 to 1 s post-stimulus). There was also a small association with reaction times in occipital channels around 1.5 seconds post-stimulus. Results were similar for the offset parameter, with an additional effect of load and n-back × stimulus type interaction (Figure S4).

Disentangling periodic and aperiodic components in EEG activity: avoiding baseline correction

EEG data analysis in our study shows that when baseline correction is applied to the total EEG activity, changes in alpha, beta and theta activity are observed following stimulus presentation (Figure 3B) compared to the pre-stimulus interval. In particular, there is a significant increase in theta power after the stimulus, while a decrease in power in the alpha-beta spectrum is observed for some time after the stimulus presentation. These findings are consistent with previous n-back studies reporting that the presentation of both target and non-target stimuli elicited long-lasting increases in theta power and decreases in alpha/beta power at stimulus onset (Palomäki et al., 2012; Krause et al., 2010; Coleman et al., 2023).

Omitting baseline correction and decomposing the total EEG activity into periodic and aperiodic components provides a more nuanced insight into the dynamics of the spectra, showing that alpha and beta activities remain oscillatory while the theta activity "disappears" from the periodic component. We find that the apparent theta activity, rather than oscillatory activity, reflects changes in the aperiodic component, which is manifested as a post-stimulus increase in theta power under baseline correction in time-frequency analysis of the full EEG spectrum. Given our current understanding of aperiodic activity, specifically based on the findings of post-stimulus slope steepening in the context of increased cognitive demands (Akbarian et al., 2023; Gyurkovics et al., 2022; Virtue-Griffiths et al., 2022), our results suggests that the change in theta-range activity is a result of aperiodic slope modulation rather than a significant increase in oscillatory activity within the theta band. In contrast, alpha and beta activity remain present as part of the periodic component throughout the task.

Our results clearly indicate that the classical baseline correction approach can subtract a significant amount of continuous periodic activity, while aperiodic activity is ignored as stationary and may even be misinterpreted as an increase in post-stimulus theta oscillations.

The modulation of periodic activity is concentrated in the alpha and beta bands

When decomposing the EEG signal into periodic and aperiodic components we still observed a significant attenuation in the power of alpha and beta oscillations after stimulus presentation (see Figure 3B, C and Figure 4A). This is in line with existing literature that documents the decrease of post-stimulus alpha and beta (Krause et al., 2010; Coleman et al., 2023). Moreover, our results support previously reported increased suppressive response that is elicited by target stimuli compared to non-target stimuli (Palomäki et al., 2012; Peng et al., 2015), especially in the alpha range (Figure S2).

Our findings support existing research (Pesonen et al., 2007) by demonstrating that reductions in alpha and beta powers are more pronounced and have longer duration under increased task demands, as is typical of higher loads in n-back tasks (see Figure 5). Consistent with seminal work (Gevins et al., 1997; Pesonen et al., 2007; Krause et al., 2010), our data show that working memory load mainly affects alpha/beta power in the parietal-occipital electrodes (see Figure 4B). In n-back tasks, diminished alpha power is thought to indicate increased engagement in working memory operations (Haegens et al., 2014). The functional significance of beta oscillations remains a topic of debate, with studies often linking centrally located beta oscillations to the coordination of motor responses (e.g. Pavlov and Kotchoubey, 2022; Pfurtscheller et al., 1998; Kaiser et al., 2001). However, recent research indicates that they also play a crucial role in working memory, particularly in supporting the maintenance of memorised information and preventing distractions (Schmidt et al., 2019; HajiHosseini et al., 2020). Additionally, beta oscillations are believed to facilitate the manipulation of stored information, dynamically adjusting to meet task demands and to serve a gating function by inhibiting irrelevant inputs, thus enhancing cognitive efficiency (ElShafei et al., 2022; Schmidt et al., 2019).

The strong correlation between alpha and lower beta range activities in central regions, as shown in Figure 5, which also aligns with reaction times, indicates that beta activity, typically associated with motor functions, is most pronounced in the central electrodes. We also observed alpha/beta activities in the posterior regions, which support current theories that suggest a collaborative function for alpha and beta oscillations in supporting advanced cognitive functions such as working memory (Scharinger et al., 2017; Coleman et al., 2023; Hanslmayr et al., 2016).

In contrast, our analyses show that theta-range activities do not necessarily exhibit an oscillatory characteristic during the n-back task (see Figure 3C, D, Figure 4). After thorough evaluation at the individual level (Figure S1), we found that only two participants exhibited evident theta peak, while only one participant exhibited pronounced theta and alpha peaks. The majority of participants exhibited alpha peaks, while only two participants displayed a theta peak and no substantial alpha activity. This suggests the presence of a low-frequency activity associated with the cognitive demands of the n-back task which might be related to the same cognitive process, but there is notable between-subject and potential within-subject variability depending on task demands.

Aperiodic activity dynamics and their cognitive implications

Our analysis of aperiodic activity at each time point within the peristimulus interval builds upon prior research that has documented stimulus-induced changes in the aperiodic component, specifically the post-stimulus steepening of the spectral slope (Gyurkovics et al., 2022; Virtue-Griffiths et al., 2022; Kałamała et al., 2024). Our data indicate the presence of two components in the dynamics of the aperiodic slope during the n-back task, differentiated both temporally and spatially.

In terms of temporality, the first component appears early in the task cycle, whereas the second component appears at a later stage (see Figure 6A). The presence of these components differs between target and non-target stimuli, with a more pronounced difference for the second component (see Figure 7). While non-target stimuli consistently exhibit a clear second component, in the case of target stimuli, the slope returns to its baseline steepness more quickly, with a significantly reduced or non-existent second slope steepening. This raises the question of whether the two components represent distinct cognitive operations inherent to the n-back task.

We speculate that the second component that emerges with greater prominence following non-target stimuli may be indicative of an elevated state of vigilance. It is uncommon for a target stimulus to be immediately succeeded by another; typically, a non-target stimulus follows. Consequently, participants may become accustomed to a period of 'rest' following a target stimulus, as the anticipation for another is low. The increased slope of the aperiodic activity may be indicative of the level of alertness for potential target stimuli. In contrast, after target stimuli, a reduction in alertness follows, leading to a quicker return to baseline, with no significant second increase in slope steepness.

As previously stated, the two aperiodic components also exhibit distinct spatial manifestations. The first component is predominantly observed on the frontal electrodes, wheres the second component is also present in the posterior channels. This difference in topography further supports the hypothesis that the two components reflect different cognitive processes. The activation in the parietal channels may be related to anticipatory mechanisms for the next stimulus, whereas the activation in the frontal channels may be involved in the decision-making process regarding the classification of the previous stimulus as a target.

Overall, our results strongly suggest that solely examining total EEG power or oscillatory dynamics, without distinctively analysing the aperiodic slope dynamics, would overlook a subtle yet potentially significant cognitive processing feature. This feature may be related to distinct working memory processes, which warrants further research.

Importantly, to exclude the possibility that aperiodic activity simply reflects the task-evoked EEG activity (i.e., event-related potentials; ERPs; see Figure S5), ERPs were subtracted before performing the time-frequency decomposition. We observed low correlations between the ERPs and aperiodic activity (Figure S6, Figure S3), suggesting that the task demands within the n-back paradigm manifest in aperiodic modulations that are distinct from other evoked EEG activity. Our findings are consistent with previous research that has consistently observed systematic, stimulus-induced changes in the aperiodic component that are distinct from concurrent stimulus-evoked EEG activity (Gyurkovics et al., 2022; Kałamała et al., 2024; Virtue-Griffiths et al., 2022). Our findings further highlight the importance of acknowledging the unique characteristics of aperiodic activity, particularly in the context of the n-back task.

Interplay of periodic and aperiodic EEG components

The relationship between periodic and aperiodic EEG activities during the n-back task reveals a complicated pattern of cognitive engagement. Following stimulus presentation, our analysis, shows an almost immediate aperiodic slope increase in the fronto-central channels (see Figure 6), followed by a brief alpha/beta attenuation in the posterior channels (see Figure 4). Both of these features have been associated with inhibitory processes that temporarily disrupt ongoing excitatory activity to allow the brain to engage with the presented stimulus (Gyurkovics et al., 2022; Kałamała et al., 2024; Gevins et al., 1997; Pesonen et al., 2007). Our results show that both the alpha/beta suppression and the aperiodic change in slope are more pronounced after tar-

get stimuli compared to non-target stimuli (see Figure 5 and Figure 7). These observations may indicate greater cognitive engagement associated with decision-making processes following the onset of the target stimulus.

Further analysis of our data shows a significant difference between the 0-back and 2-back conditions in the periodic component (Figure 5), indicating more sustained alpha/beta suppression in the 2-back condition, whereas the aperiodic component did not show such spectral slope differences. Sustained suppression of periodic alpha and beta activity during the 2-back condition may reflect ongoing active engagement in the form of information encoding, retention, and updating. This finding suggests that the periodic and aperiodic components may reflect distinct cognitive processes. The characteristics of the second component in the aperiodic slope after non-target stimuli (see Figure 6), with no obvious co-occurring processes in the periodic component, further support this idea. It is important to analyse both components to ensure that the processes they reflect are not overlooked.

Our data show a clear distinction between the periodic and aperiodic components in relation to reaction times. Our results support the association between central beta activity and motor planning (e.g. Eggermont, 2021; Pfurtscheller et al., 1998), as evidenced by its correlation with reaction times in our analysis of the periodic component (Figure 5). In contrast, our analysis indicates a weak correlation between the dynamics of the aperiodic component and reaction times (Figure 7). This observation differs from the most commonly reported patterns (e.g. Voytek et al., 2015; Thuwal et al., 2021; Akbarian et al., 2023), but the evidence remains inconclusive, as some studies have reported contrasting results (e.g. Monchy et al., 2023)). The discrepancy highlights the need for further research to understand how different factors influence the manifestation of the aperiodic component as a reflection of cognitive processes.

Prior studies have consistently reported sustained elevations in theta power during the n-back task (e.g. Palomäki et al., 2012; Krause et al., 2010; Pesonen et al., 2007). These increases, particularly in the frontal cortex, have been linked to various cognitive functions such as attention, information encoding, and cognitive control (Roux and Uhlhaas, 2014; Rossi et al., 2023; Cavanagh and Frank, 2014). While theta activity can indeed be oscillatory, as demonstrated in some studies, the sustained theta activity observed in our scalp EEG data (Figure 3) appears predominantly aperiodic, with post-stimulus increases more likely attributable to shifts in spectral slope than to oscillatory changes. Theta activity can represent either oscillatory or aperiodic activity, but careful distinction between these components is necessary to avoid potential misinterpretation of theta dynamics. Nevertheless, previously reported patterns of theta modulation are consistent with the notion that post-stimulus changes in aperiodic activity may reflect enhanced inhibitory control commensurate with task demands (Voytek et al., 2015; Gao et al., 2017).

Analyses of control data from a previously published study (Nakuci et al., 2023) confirmed our initial results, indicating that similar task-related modulations in alpha and beta periodic activities, as well as aperiodic activity dynamics, can be divided into frontal and parietal components. However, although both aperiodic components were observed in the alternative dataset, their temporal differentiation was less pronounced (Figure S12, Figure S14). Notably, in this comparative dataset the exponent was only related to task load, with an increased exponent for the 2-back level, and not to stimulus type (Figure S13). Furthermore, in the comparative dataset there was an association with reaction times in the parietal channels, more so than in our original dataset. Nevertheless, the results of the control analysis serve to reinforce the robustness of our insights. In particular, the similarities observed in the modulation of theta-like activity attributed to aperiodic shifts provide a crucial validation of our conclusions regarding the nature of theta activity and the aperiodic component.

Theoretical and methodological implications

Our study highlights the need for refined EEG analysis methods that take into account the dynamic nature of both periodic and aperiodic components during cognitive tasks. Our findings indicate a need for a methodological shift in baseline correction techniques, particularly in continuous cognitive tasks where traditional baseline substraction can obscure significant neural dynamics by misrepresenting aperiodic activity as theta-band oscillatory activity (Gyurkovics et al., 2021). This misrepresentation is of importance, as baseline corrections, designed to normalise data, may inadvertently distort the true nature of neural activities, especially under conditions of sustained cognitive demand. Further investigation is warranted to explore how changes in the aperiodic component's slope might underlie the commonly observed increases in frontal theta activity, traditionally documented as theta oscillations. In order to validate this hypothesis, future research should extend to a wider range of working memory and cognitive control tasks.

The aperiodic slope dynamics observed during the n-back task in our study align with the E:I balance framework (Gao et al., 2017; Vogels and Abbott, 2009; Lim and Goldman, 2013). Specifically, our results suggest that stimulus-induced shifts in the aperiodic slope likely reflect a proportional modulation of ongoing excitatory activities tailored to meet processing demands (Gyurkovics et al., 2022; Voytek et al., 2015; Virtue-Griffiths et al., 2022). These adjustments in the post-stimulus aperiodic component may signify enhanced inhibitory control, which has implications for cognitive control capacities previously associated with changes in the frontal theta-band activity (e.g. Scharinger et al., 2017; Cavanagh and Frank, 2014; Ratcliffe et al., 2022).

Our findings provide support for the hypothesis that modifications in aperiodic activity following cognitive load could serve as a reliable index of cognitive control mechanisms. Future studies should consider aperiodic dynamics as a potential biomarker for cognitive control, investigating how these measures correlate with traditional indicators and whether they can predict cognitive performance across different task contexts.

To better understand the functional role of the observed second component in the aperiodic activity (second slope steepening) following non-target trials, a study design incorporating a larger dataset with an increased number of target-followed-by-target sequences is essential. This would enable a detailed comparison of aperiodic slope components in scenarios where a target is succeeded by another target versus when it is followed by a non-target, potentially revealing how attentional mechanisms are reset or sustained under different conditions.

Furthermore, investigating the interplay between aperiodic slope dynamics and theta oscillations in tasks requiring enhanced cognitive control could provide deeper insights into the neural basis of cognitive flexibility and decision-making. It is also imperative to consider individual variations in theta range dynamics and their relationship with aperiodic slope modulation, as this could highlight potential biomarkers for cognitive efficiency or susceptibility to cognitive fatigue.

Finally, our findings challenge the established methodologies and interpretations of EEG-measured cross-frequency coupling, particularly phase-amplitude coupling (Tort et al., 2010; Van Der Meij et al., 2012; Tseng et al., 2019). While numerous studies have demonstrated the modulation of gamma amplitude by the phase of theta (e.g. Park et al., 2013; Köster et al., 2014; Goodman et al., 2018), which is believed to organise information in working memory (e.g. Rajji et al., 2016; Brooks et al., 2020; McGill and Kieffaber, 2024; Goodman et al., 2018), our findings suggest that theta dynamics, as measured with scalp EEG, are predominantly a result of aperiodic shifts. Consequently, it may not always be appropriate to assume that theta activity is inherently oscillatory when analysing phenomena such as theta-gamma coupling. This observation challenges the traditional interpretation of how theta and gamma activities interact during cognitive processes. To ensure accuracy in future studies of cross-frequency coupling such as theta-gamma coupling, it is crucial to verify that theta activity is truly oscillatory before proceeding with analyses.

Strengths and limitations

The main strength of our study lies in the replication of key findings by performing the same analyses on an independent sample of younger individuals engaged in a standard verbal n-back task. This replication extends the generalisability of our results beyond the initial cohort of older adults. The methodological rigour and consistency of the results add to the credibility of our findings.

There are a number of limitations that need to be considered. First, the task difficulty in the 2-back condition may have been too high. Some participants had to be excluded from the analysis due to poor performance. This exclusion may have reduced the range of cognitive abilities in the sample of older adults, potentially inflating them.

In addition, the higher level of difficulty in the tasks may have influenced the observed differences between the 0-back and 2-back conditions, potentially affecting the magnitude and direction of the reported neural modulations. For our sample of older adults, a simplified 2-back task using a single modality may have been more appropriate. The single modality (verbal, with letters displayed in the centre of the screen) may help to reduce task complexity and align better with the cognitive abilities of older participants. In addition, the dual-modality task imposed time constraints that limited the number of trials for each condition, potentially leading to participant fatigue and reduced data quality.

Conclusions

Our study highlights the critical importance of distinguishing between the periodic and aperiodic components of the EEG spectrum in order to ensure accurate interpretation of changes traditionally attributed to oscillatory activity. Using the n-back task, we have demonstrated that the aperiodic component, which is often dismissed as mere background noise, reflects important features of cognitive processing. Our findings also challenge the routine practice of baseline correction, which can obscure crucial modulations of aperiodic activity, particularly in continuous cognitive tasks. It is important to note that a considerable proportion of the theta activity commonly observed in scalp EEG may actually be due to shifts in the aperiodic slope. It is therefore essential to independently verify whether the observed theta activity is genuinely oscillatory or primarily aperiodic. This is of utmost importance for accurately deciphering the neural underpinnings of working memory and cognitive control, and indicates a need for a paradigm shift in the analysis and interpretation of EEG data.

Methods

Participants

We analysed EEG recordings from fifty-seven volunteers (nine males) aged 55–78 years (M = 67.4, SD ± 6.4), who initially participated in a study on subjective cognitive complaints. All participants had normal or corrected-to-normal vision and were free from neurological or psychiatric illness or cognitive decline, as assessed by neuropsychological testing prior to study entry. Of these participants, twenty-seven reported subjective cognitive complaints, while thirty did not. Our current study focused exclusively on within-subject

comparisons and did not investigate subjective cognitive complaints or between-group differences. We excluded data from 10 participants from all analyses due to poor quality.

The study protocol was approved by the Medical Ethics Committee of the Republic of Slovenia (protocol number 0120-128/2019/9; 21.08.2019). All study participants gave written informed consent prior to the initiation of any study-related procedures.

Experimental task and procedure

The participants were instructed to press the left button when the letter or position matched the letter/position n-back trials before (i.e. on target trials), and the right button otherwise (on non-target trials). Some of the stimuli were lures, i.e. stimuli that would have been considered targets in the 1-back condition but appeared during the 2-back condition.

The participants completed the n-back task in two modalities (visuospatial and verbal) with two load conditions (0- and 2-back) (Figure 1). During the task, participants were presented with white capital letters on a grey background one at a time in one of nine possible positions, in a continuous sequence. Each letter was presented on the screen for 250 ms, followed by a 3000 ms interval during which participants were required to respond. In the verbal task conditions, participants were instructed to memorise the presented letter, whereas in the visuospatial task conditions, participants were asked to memorise the position of the presented letter. The order of modality was counterbalanced across participants.

Each modality always began with the 0-back load condition in which the target stimulus was presented for 10 seconds at the beginning of the block and stayed the same throughout the whole block. The 0-back load condition was followed by a 2-back load condition of the same modality, where participants had to remember each stimulus as it appeared and discern whether it matched the one displayed two trials prior. The 0-back and 2-back load conditions each comprised three 5-minute blocks of continuously presented stimuli. For each modality, the 0-back load condition comprised a total of 201 stimuli, 39 of which were targets, and the 2-back load condition comprised a total of 240 stimuli, 39 of which were targets, and 30 were lures. All stimuli were presented in a pseudorandomised order.

The task began only after participants indicated their readiness by pressing a designated key, after reviewing the instructions and clarifying any doubts with the experimenter. Before each condition, participants completed a practice session consisting of a short block to familiarise themselves with the task demands. The session included a variation of the main task in which participants practised identifying both the target letter and its location, as well as responding to the 2-back challenge for both letters and positions. During the main task, response accuracy and reaction times were recorded by keystroke on the Cedrus response pad (Cedrus Corporation, San Pedro, CA, USA, model RB-540). Participants were instructed to favour accurate responses over fast responses. The participants' responses were monitored, and only trials with correct responses were included in the EEG analysis.

The stimuli were presented in Helvetica font on a 24-inch LCD screen with a refresh rate of 120 Hz. The stimuli, arranged in a 3 $\times$ 3 matrix, spanned approximately 7.22 degrees of both vertical and horizontal visual angles. The task was programmed and executed using PsychoPy 3 (Peirce et al., 2022).

EEG data acquisition

We recorded EEG activity using either a BrainAmp MR-plus or ActiChamp amplifier (Brain Products GmbH, Germany). We acquired the recordings with a 64-channel ActiCap plus a reference channel, configured according to the extended 10-10 international system layout. To accommodate all participants, we used two slightly different electrode layouts, differing only in the position of two electrodes. Due to inconsistencies in electrode placement between subjects, we excluded channels AFz, Iz, PO9, and PO10 from the analysis, resulting in a dataset of 63 electrodes (including the reference channel). We grounded the electrode setup at AFz, with FCz serving as the reference. During the EEG recording, we band-pass filtered the signal between 0.1 and 250 (or 1000) Hz with a slope of 12dB/octave and digitised it at a sampling rate of 500, 1000, or 2500 Hz. After time-frequency decomposition, we downsampled the data to 100 Hz.

EEG data preprocessing

We preprocessed the EEG data using custom MATLAB scripts (MathWorks, USA) that integrated functions from EEGLAB (Delorme and Makeig, 2004) and ERPLAB (Lopez-Calderon and Luck, 2014). High-pass filtering at 0.1 Hz was performed using a finite impulse response (FIR) filter (2nd order Butterworth, slope: 12 dB/octave). A CleanLine filter was then used to reduce power line noise at 50 Hz (Mullen, 2012). Next, we segmented the data into epochs ranging from -1.5 to 2.8 seconds, time-locked to stimulus presentations, followed by baseline correction to remove residual signal drift. Epochs and channels were manually inspected to identify and exclude segments with excessive artefacts. Independent component analysis decomposition was performed using the AMICA algorithm (Palmer et al., 2011), applied to the data bandpass filtered between 1 and 60 Hz; the solution was later applied to the non-bandpass filtered data. We manually inspected the independent components to identify and remove those representing blinks, horizontal eye movements, muscle noise, line noise, and other artefacts. After the ICA, channel time series reconstruction and channel interpolation were performed, and the data were referenced to the average reference.

Subsequent EEG analyses were conducted only on subjects and conditions that met the required standards, defined as having a minimum of 30 good epochs after cleaning and an accuracy rate of at least 0.6 within a given condition. Exclusion criteria were applied at the level of individual conditions within subjects, rather than excluding entire participants from the analyses. Consequently, only 21% and 10% of participants remained for the visuospatial and verbal lure conditions, respectively. As a result, the lure condition was excluded from all subsequent analyses.

Estimation of periodic and aperiodic component

First, we excluded trials with incorrect or missing responses from all subsequent analyses. ERPs related to early sensory potentials can affect estimates of aperiodic activity (Gyurkovics et al., 2022), therefore, average ERPs were removed prior to time-frequency decomposition, as has been previously done in similar studies (Gyurkovics et al., 2022; Kałamała et al., 2024). This involved computing ERPs for each subject/condition and then subtracting these ERPs from single-trial data for each subject/condition.

To estimate both periodic and aperiodic components of EEG activity, we performed time-frequency decomposition using superlets, with a range of frequencies from 3 to 50 Hz, in steps of 1 Hz (width of the base wavelet: 3 cycles, order: linearly spaced from 1 to 20, multiplicative combination of wavelets) as implemented in Fieldtrip (Oostenveld et al., 2011). Superlets, a variant of the Morlet wavelet transformation, involve multiple decompositions with varying cycles, the results of which are combined using a geometric mean to achieve enhanced temporal and spectral resolution, known as 'super-resolution' (Moca et al., 2021). The results of the time-frequency decomposition were averaged for each condition and participant, and then decimated to 100 Hz in order to save space and facilitate further analysis.

We then estimated the periodic and aperiodic components from the decomposed data for each time point, condition, and participant using the FOOOF algorithm from the Python specparam package (Donoghue et al., 2020b). To avoid edge artefacts, FOOOF parameters were estimated for a period between -0.5 and 2 seconds around the stimulus. The FOOOF algorithm estimates the frequency spectrum in a semi-log space (i.e. only power is log-transformed) using a set of parameters separately for periodic and aperiodic activity. Specifically, neural power spectra (NPS) over a set of frequencies (F) are described as the sum of the aperiodic and periodic components:

$$NPS(F) = L(F) + G(F)_n \quad \textbf{(1)}$$

The aperiodic component is modelled as

$$L(F) = b - \log(k + F^{\chi}) \quad \textbf{(2)}$$

where b is the offset, k is the knee (bend), and χ is the exponent (slope).

The periodic component is modelled as a sum of Gaussians:

$$G(F)_n = a * \exp\left(\frac{-(F-c)^2}{2*w^2}\right) \quad \textbf{(3)}$$

Each Gaussian is described by three parameters: c, a, and w, representing center frequency, power, and bandwidth, respectively.

Fitting was performed using default specparam parameters: peak width limits = 0.5–12.0 Hz, maximum number of peaks to fit = Inf, minimum peak height = 0, peak threshold = 2.0, aperiodic mode = 'fixed' (i.e. the knee parameter was set to 0). The outcomes of the analyses conducted with the offset and exponent parameters were found to be highly comparable. Consequently, the results presented in the main text pertain solely to the analyses conducted with the exponent parameter, while those in the Supplement pertain to the offset parameter.

To allow comparisons with full time-frequency power and to facilitate comparisons across participants and conditions, we reconstructed the periodic component in a semi-log space based on the estimated parameters for each participant and condition.

We visually assessed time-frequency plots both in their original form and following baseline correction (decibel transformation) before conducting formal statistical analyses. We also compared these plots with those of periodic and aperiodic activity. Additionally, we visualised the periodic activity, averaged over time, for each participant (Figure S1, Figure S1).

Statistical analysis

We conducted statistical comparisons using linear mixed models with the $fitlme$ function in MATLAB. One advantage of using linear mixed models is their ability to accommodate missing data, which improves parameter estimates through partial pooling. We fitted the models as follows:

$$y \sim 1 + modality * nback * stimulus + rt + (1|subject) \quad \textbf{(4)}$$

Here, y refers to the exponent or offset in the case of aperiodic activity and to the log-power in the case of periodic activity. We included reaction times (rt) in the model to control for differences between conditions and to assess the relationship between motor response and EEG activity.

To estimate representative reaction times for each participant and condition, we removed reaction times above a z-value of 3 and those below 200 ms (within each participant and condition). Next, we fitted an ex-Gaussian distribution to estimate the parameter μ using the maximum likelihood method as implemented in the retimes package in R (Massidda, 2013). The ex-Gaussian distribution, a positively skewed distribution, is useful for describing reaction time distributions

(Balota and Yap, 2011), and the parameter μ can be interpreted as the mode of the distribution.

We fitted models in a mass univariate manner, that is for each channel, frequency (where applicable), and time point separately.

The maximum likelihood method estimated the fixed effects, and the degrees of freedom were approximated using the Satterthwaite equation. The p-values underwent correction using the Benjamini-Yekutieli false discovery rate (FDR) correction (Benjamini and Yekutieli, 2001). Given that under the false discovery rate (FDR) correction, a q proportion of significant p-values are false positives, and that EEG effects occur in clusters (in time, frequency, and/or space) (Van Ede and Maris, 2016), we additionally considered as significant only clusters of p-values that spanned either at least three time points or at least three channels. We set the significance threshold at $\alpha = .05$.

For the purposes of visualisation, p-values were averaged across channels (for heatmaps or lines) or across time (for topographies). Consequently, there are some discrepancies between heatmaps/lines and topographies.

Comparison of aperiodic activity with event-related potentials

To rule out the possibility that aperiodic activity merely reflected evoked potentials, we first removed evoked activity before time-frequency decomposition (as described above). We then computed Pearson correlations between event-related potentials (ERPs) and aperiodic activity across channels for each condition, subject and time point. The results are shown in the Supplement.

Control analysis

To test the generalisability of the results, we repeated the analyses using an alternative EEG dataset from a previously published study by Nakuci et al. (2023). This dataset includes data from 21 subjects (17 female, mean age 42 $\pm$ 12 years) who performed a verbal n-back task (0-, 1-, and 2-back) while being recorded with a 256-channel HydroCel Geodesic Sensor Net. The task involved 150 trials per condition, 50 of which were targets. Each stimulus was presented for 400 ms, followed by an interstimulus interval of 2000 ms.

The dataset was utilised in its preprocessed form, as the unprocessed data were unavailable. The preprocessing included band-pass filtering, artifact subspace reconstruction (ASR) (Mullen et al., 2013), independent component analysis, channel interpolation, another round of ASR, re-referencing to the average reference, epoching from -1000 to 2000 ms around stimulus presentation, and baseline correction using the prestimulus period (Nakuci et al., 2023). Notably, data were band-pass filtered between 0.5 and 50 Hz, limiting the time-frequency decomposition and FOOOF analysis to frequencies between 3 and 35 Hz.

We carried out all other analytical steps, including time-frequency decomposition, FOOOF analysis, and statistical comparisons, in the same manner as in the primary analysis.

The results of this control analysis are presented in the Supplement.

Data and code availability

The preprocessed data are available at https://dx.doi.org/10.17605/OSF.IO/RQ8ZM. The alternative EEG dataset (Nakuci et al., 2023) is available at https://zenodo.org/records/6897260.

Preprocessing was performed using EEGLAB (https://github.com/sccn/eeglab) and EEGLAB plugins. Time-frequency decomposition was performed using the Fieldtrip function $ft_freqanalysis$ (https://github.com/fieldtrip/fieldtrip/blob/master/ft_freqanalysis.m). FOOOF decomposition was performed using the Python package specparam (https://github.com/fooof-tools/fooof/). Linear mixed models were estimated using the MATLAB function $fitlme$ (https://www.mathworks.com/help/stats/fitlme.html). Visualisation was done using the packages ggplot2 (https://ggplot2.tidyverse.org/), matplotlib (https://matplotlib.org/) and MNE-Python (https://mne.tools/).

Acknowledgments

The authors would like to thank Zvezdan Pirtošek for the help with project management, Katarina Marjanovič, Aleš Oblak, Katarina Sinja Miloševič, Tala Koren, Anja Čuš, Nina Lang, Taja Žnidarič, Dunja Kolenko, Irena Hostnikar, Urška Levac, Matija Kuclar, Vesna Muzek, Klara Babič, Kristina Klančič, Sara Bugarinovič and Lea Kukovec for the help with the data collection. The authors would also like to thank the participants, without whom this study would not have been possible.

Funding sources

The research was funded by the following ARIS grants: J3-8200 (TF, AM, TM, JB), P5-0110 (AM, JB), P3-0338 (GR), J5-4590 (AM, GR, JB), and J3-9264 (AM, GR, TM).

Author contributions

Tisa Frelih: Conceptualization, Project administration, Data curation, Investigation, Methodology, Visualization, Writing – original draft, Writing – review and editing; Andraž Matkovič: Conceptualization, Investigation, Formal analysis, Methodology, Software, Data curation, Visualization, Writing – original draft, Writing – review and editing; Tjaša Mlinarič: Investigation, Project administration, Writing – review and editing; Jurij Bon:

Resources, Supervision, Writing – review and editing; Grega Repovš: Conceptualization, Methodology, Software, Resources, Supervision, Writing – review and editing.

Conflicts of interest

G.R. consults for and holds equity in Neumora and Manifest Technologies. A.M. has previously consulted for Neumora.

References

Ahmad, J., Ellis, C., Leech, R., Voytek, B., Garces, P., Jones, E., Buitelaar, J., Loth, E., dos Santos, F. P., Amil, A. F., Verschure, P. F. M. J., Murphy, D., and McAlonan, G. (2022). From mechanisms to markers: novel noninvasive EEG proxy markers of the neural excitation and inhibition system in humans. *Translational Psychiatry*, 12(1):1–12. doi: 10.1038/s41398-022-02218-z.

Akbarian, F., Rossi, C., Costers, L., D'hooghe, M. B., D'haeseleer, M., Nagels, G., and Van Schependom, J. Stimulus-related modulation in the 1/f spectral slope suggests an impaired inhibition of irrelevant information in people with multiple sclerosis. preprint, Neuroscience, (2023). URL http://biorxiv.org/lookup/doi/10.1101/2023.12.28.573572.

Baddeley, A. (2012). Working Memory: Theories, Models, and Controversies. *Annual Review of Psychology*, 63(1):1–29. doi: 10.1146/annurev-psych-120710-100422. _eprint: https://doi.org/10.1146/annurev-psych-120710-100422.

Balota, D. A. and Yap, M. J. (2011). Moving Beyond the Mean in Studies of Mental Chronometry: The Power of Response Time Distributional Analyses. *Current Directions in Psychological Science*, 20(3):160–166. doi: 10.1177/0963721411408885.

Benjamini, Y. and Yekutieli, D. (2001). The control of the false discovery rate in multiple testing under dependency. *The Annals of Statistics*, 29(4). doi: 10.1214/aos/1013699998.

Brooks, H., Goodman, M. S., Bowie, C. R., Zomorrodi, R., Blumberger, D. M., Butters, M. A., Daskalakis, Z. J., Fischer, C. E., Flint, A., Herrmann, N., Kumar, S., Mah, L., Mulsant, B. H., Pollock, B. G., Voineskos, A. N., and Rajji, T. K. (2020). Theta–gamma coupling and ordering information: a stable brain–behavior relationship across cognitive tasks and clinical conditions. *Neuropsychopharmacology*, 45(12):2038–2047. doi: 10.1038/s41386-020-0759-z.

Bullock, T. H., Mcclune, M. C., and Enright, J. T. (2003). Are the electroencephalograms mainly rhythmic? Assessment of periodicity in wide-band time series. *Neuroscience*, 121 (1):233–252. doi: 10.1016/S0306-4522(03)00208-2.

Cavanagh, J. F. and Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. *Trends in Cognitive Sciences*, 18(8):414–421. doi: 10.1016/j.tics.2014.04.012.

Chen, Y. and Huang, X. (2016). Modulation of Alpha and Beta Oscillations during an n-back Task with Varying Temporal Memory Load. *Frontiers in Psychology*, 6:2031. doi: 10.3389/fpsyg.2015.02031.

Cohen, M. X. *Analyzing Neural Time Series Data: Theory and Practice*. The MIT Press, (2014). ISBN 978-0-262-31955-3. doi: 10.7551/mitpress/9609.001.0001.

Coleman, S. C., Seedat, Z. A., Whittaker, A. C., Lenartowicz, A., and Mullinger, K. J. (2023). Beyond the Beta Rebound: Post-Task Responses in Oscillatory Activity follow Cessation of Working Memory Processes. *NeuroImage*, 265:119801. doi: 10.1016/j.neuroimage.2022.119801.

Dave, S., Brothers, T. A., and Swaab, T. Y. (2018). 1/f neural noise and electrophysiological indices of contextual prediction in aging. *Brain Research*, 1691:34–43. doi: 10.1016/j.brainres.2018.04.007.

Delorme, A. and Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1):9–21. doi: 10.1016/j.jneumeth.2003.10.009.

Donoghue, T., Dominguez, J., and Voytek, B. (2020). Electrophysiological Frequency Band Ratio Measures Conflate Periodic and Aperiodic Neural Activity. *eNeuro*, 7(6). doi: 10.1523/ENEURO.0192-20.2020. Publisher: Society for Neuroscience Section: Research Article: New Research.

Donoghue, T., Haller, M., Peterson, E. J., Varma, P., Sebastian, P., Gao, R., Noto, T., Lara, A. H., Wallis, J. D., Knight, R. T., Shestyuk, A., and Voytek, B. (2020). Parameterizing neural power spectra into periodic and aperiodic components. *Nature Neuroscience*, 23 (12):1655–1665. doi: 10.1038/s41593-020-00744-x.

Donoghue, T., Schaworonkow, N., and Voytek, B. (2022). Methodological considerations for studying neural oscillations. *European Journal of Neuroscience*, 55(11-12):3502–3527. doi: 10.1111/ejn.15361.

Eggermont, J. J. Chapter 2 - The gamma, beta, and theta rhythms and nested oscillations. In Eggermont, J. J., editor, *Brain Oscillations, Synchrony, and Plasticity*, pages 23–42. Academic Press, (2021). ISBN 978-0-12-819818-6. doi: 10.1016/B978-0-12-819818-6.00014-5. URL https://www.sciencedirect.com/science/article/pii/B9780128198186000145.

ElShafei, H. A., Zhou, Y. J., and Haegens, S. (2022). Shaping Information Processing: The Role of Oscillatory Dynamics in a Working Memory Task. *eNeuro*, 9(5). doi: 10.1523/ENEURO.0489-21.2022.

Gao, R., Peterson, E. J., and Voytek, B. (2017). Inferring synaptic excitation/inhibition balance from field potentials. *NeuroImage*, 158:70–78. doi: 10.1016/j.neuroimage.2017.06.078.

Gevins, A., Smith, M. E., McEvoy, L., and Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. *Cerebral Cortex*, 7(4):374–385. doi: 10.1093/cercor/7.4.374.

Goodman, M. S., Kumar, S., Zomorrodi, R., Ghazala, Z., Cheam, A. S. M., Barr, M. S., Daskalakis, Z. J., Blumberger, D. M., Fischer, C., Flint, A., Mah, L., Herrmann, N., Bowie, C. R., Mulsant, B. H., and Rajji, T. K. (2018). Theta-Gamma Coupling and Working Memory in Alzheimer's Dementia and Mild Cognitive Impairment. *Frontiers in Aging Neuroscience*, 10. doi: 10.3389/fnagi.2018.00101.

Gyurkovics, M., Clements, G. M., Low, K. A., Fabiani, M., and Gratton, G. (2021). The impact of 1/f activity and baseline correction on the results and interpretation of time-frequency analyses of EEG/MEG data: A cautionary tale. *NeuroImage*, 237:118192. doi: 10.1016/j.neuroimage.2021.118192.

Gyurkovics, M., Clements, G. M., Low, K. A., Fabiani, M., and Gratton, G. (2022). Stimulus-Induced Changes in 1/ *f* -like Background Activity in EEG. *The Journal of Neuroscience*, 42(37):7144–7151. doi: 10.1523/JNEUROSCI.0414-22.2022.

Haegens, S., Cousijn, H., Wallis, G., Harrison, P. J., and Nobre, A. C. (2014). Inter- and intra-individual variability in alpha peak frequency. *NeuroImage*, 92:46–55. doi: 10.1016/j.neuroimage.2014.01.049.

HajiHosseini, A., Hutcherson, C. A., and Holroyd, C. B. (2020). Beta oscillations following performance feedback predict subsequent recall of task-relevant information. *Scientific Reports*, 10(1):15114. doi: 10.1038/s41598-020-72128-x. Publisher: Nature Publishing Group.

Hanslmayr, S., Staresina, B. P., and Bowman, H. (2016). Oscillations and Episodic Memory: Addressing the Synchronization/Desynchronization Conundrum. *Trends in Neurosciences*, 39(1):16–25. doi: 10.1016/j.tins.2015.11.004. Publisher: Elsevier.

He, B. J. (2014). Scale-free brain activity: past, present and future. *Trends in cognitive sciences*, 18(9):480–487. doi: 10.1016/j.tics.2014.04.003.

Kaiser, J., Birbaumer, N., and Lutzenberger, W. (2001). Event-related beta desynchronization indicates timing of response selection in a delayed-response paradigm in humans. *Neuroscience Letters*, 312(3):149–152. doi: 10.1016/S0304-3940(01)02217-0.

Kałamała, P., Gyurkovics, M., Bowie, D. C., Clements, G. M., Low, K. A., Dolcos, F., Fabiani, M., and Gratton, G. (2024). Event-induced modulation of aperiodic background EEG: Attention-dependent and age-related shifts in E:I balance, and their consequences for behavior. *Imaging Neuroscience*, 2:1–18. doi: 10.1162/imag_a_00054.

Krause, C. M., Pesonen, M., and Hämäläinen, H. (2010). Brain oscillatory 4–30 Hz electroencephalogram responses in adolescents during a visual memory task. *NeuroReport*, 21(11):767. doi: 10.1097/WNR.0b013e32833bfcbb.

Köster, M., Friese, U., Schöne, B., Trujillo-Barreto, N., and Gruber, T. (2014). Theta–gamma coupling during episodic retrieval in the human EEG. *Brain Research*, 1577:57–68. doi: 10.1016/j.brainres.2014.06.028.

Lendner, J. D., Harler, U., Daume, J., Engel, A. K., Zöllner, C., Schneider, T. R., and Fischer, M. (2023). Oscillatory and aperiodic neuronal activity in working memory following anesthesia. *Clinical Neurophysiology*, 150:79–88. doi: 10.1016/j.clinph.2023.03.005.

Lim, S. and Goldman, M. S. (2013). Balanced cortical microcircuitry for maintaining information in working memory. *Nature neuroscience*, 16(9):1306–1314. doi: 10.1038/nn.3492.

Lopez-Calderon, J. and Luck, S. J. (2014). ERPLAB: an open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, 8. doi: 10.3389/fnhum.2014.00213.

Massidda, D., (2013). URL https://CRAN.R-project.org/package=retimes.

McGill, M. B. and Kieffaber, P. D. (2024). Event-Related Theta and Gamma Band Oscillatory Dynamics During Visuo-Spatial Sequence Memory in Younger and Older Adults. *PLOS ONE*, 19(4):e0297995. doi: 10.1371/journal.pone.0297995.

Merkin, A., Sghirripa, S., Graetz, L., Smith, A. E., Hordacre, B., Harris, R., Pitcher, J., Semmler, J., Rogasch, N. C., and Goldsworthy, M. (2023). Do age-related differences in aperiodic neural activity explain differences in resting EEG alpha? *Neurobiology of Aging*, 121:78–87. doi: 10.1016/j.neurobiolaging.2022.09.003.

Moca, V. V., Bârzan, H., Nagy-Dăbâcan, A., and Mureşan, R. C. (2021). Time-frequency super-resolution with superlets. *Nature Communications*, 12(1):337. doi: 10.1038/s41467-020-20539-9.

Monchy, N., Modolo, J., Houvenaghel, J.-F., Voytek, B., and Duprez, J. Changes in electrophysiological aperiodic activity during cognitive control in Parkinson's disease. preprint, Neuroscience, (2023). URL http://biorxiv.org/lookup/doi/10.1101/2023.10.09.561166.

Mullen, T., (2012). URL https://www.nitrc.org/projects/cleanline.

Mullen, T., Kothe, C., Chi, Y. M., Ojeda, A., Kerth, T., Makeig, S., Cauwenberghs, G., and Tzyy-Ping Jung. Real-time modeling and 3D visualization of source dynamics and connectivity using wearable EEG. In *2013 35th Annual International Conference of the IEEE Engineering in Medicine and Biology Society (EMBC)*, pages 2184–2187, Osaka, (2013). IEEE. ISBN 978-1-4577-0216-7. doi: 10.1109/EMBC.2013.6609968. URL http://ieeexplore.ieee.org/document/6609968/.

Nakuci, J., Covey, T. J., Shucard, J. L., Shucard, D. W., and Muldoon, S. F. (2023). Single trial variability in neural activity during a working memory task reveals multiple distinct information processing sequences. *NeuroImage*, 269:119895. doi: 10.1016/j.neuroimage.2023.119895.

Oostenveld, R., Fries, P., Maris, E., and Schoffelen, J.-M. (2011). FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience*, 2011:1–9. doi: 10.1155/2011/156869.

Owen, A. M., McMillan, K. M., Laird, A. R., and Bullmore, E. (2005). N-back working memory paradigm: A meta-analysis of normative functional neuroimaging studies. *Human Brain Mapping*, 25(1):46–59. doi: 10.1002/hbm.20131.

Palmer, J. A., Kreutz-Delgado, K., and Makeig, S. (2011). AMICA: An Adaptive Mixture of Independent Component Analyzers with Shared Components.

Palomäki, J., Kivikangas, M., Alafuzoff, A., Hakala, T., and Krause, C. M. (2012). Brain oscillatory 4–35Hz EEG responses during an n-back task with complex visual stimuli. *Neuroscience Letters*, 516(1):141–145. doi: 10.1016/j.neulet.2012.03.076.

Park, J. Y., Jhung, K., Lee, J., and An, S. K. (2013). Theta–gamma coupling during a working memory task as compared to a simple vigilance task. *Neuroscience Letters*, 532:39–43. doi: 10.1016/j.neulet.2012.10.061.

Pavlov, Y. G. and Kotchoubey, B. (2022). Oscillatory brain activity and maintenance of verbal and visual working memory: A systematic review. *Psychophysiology*, 59(5):e13735. doi: 10.1111/psyp.13735.

Peirce, J., Hirst, R., and MacAskill, M. *Building experiments in PsychoPy*. SAGE, Los Angeles, 2nd edition edition, (2022). ISBN 978-1-5297-4166-7 978-1-5297-4165-0.

Peng, W., Hu, Y., Mao, Y., and Babiloni, C. (2015). Widespread cortical α-ERD accompanying visual oddball target stimuli is frequency but non-modality specific. *Behavioural Brain Research*, 295:71–77. doi: 10.1016/j.bbr.2015.04.051.

Pesonen, M., Hämäläinen, H., and Krause, C. M. (2007). Brain oscillatory 4–30 Hz responses during a visual n-back memory task with varying memory load. *Brain Research*, 1138: 171–177. doi: 10.1016/j.brainres.2006.12.076.

Pfurtscheller, G., Zalaudek, K., and Neuper, C. (1998). Event-related beta synchronization after wrist, finger and thumb movement. *Electroencephalography and Clinical Neurophysiology/Electromyography and Motor Control*, 109(2):154–160. doi: 10.1016/S0924-980X(97)00070-2.

Podvalny, E., Noy, N., Harel, M., Bickel, S., Chechik, G., Schroeder, C. E., Mehta, A. D., Tsodyks, M., and Malach, R. (2015). A unifying principle underlying the extracellular field potential spectral responses in the human cortex. *Journal of Neurophysiology*, 114(1): 505–519. doi: 10.1152/jn.00943.2014. Publisher: American Physiological Society.

Rajji, T. K., Zomorrodi, R., Barr, M. S., Blumberger, D. M., Mulsant, B. H., and Daskalakis, Z. J. (2016). Ordering Information in Working Memory and Modulation of Gamma by Theta Oscillations in Humans. *Cerebral Cortex*, page bhv326. doi: 10.1093/cercor/bhv326.

Ratcliffe, O., Shapiro, K., and Staresina, B. P. (2022). Fronto-medial theta coordinates posterior maintenance of working memory content. *Current Biology*, 32(10):2121–2129.e3. doi: 10.1016/j.cub.2022.03.045.

Rossi, C., Vidaurre, D., Costers, L., Akbarian, F., Woolrich, M., Nagels, G., and Van Schependom, J. (2023). A data-driven network decomposition of the temporal, spatial, and spectral dynamics underpinning visual-verbal working memory processes. *Communications Biology*, 6(1):1–12. doi: 10.1038/s42003-023-05448-z.

Roux, F. and Uhlhaas, P. J. (2014). Working memory and neural oscillations: alpha–gamma versus theta–gamma codes for distinct WM information? *Trends in Cognitive Sciences*, 18(1):16–25. doi: 10.1016/j.tics.2013.10.010.

Scharinger, C., Soutschek, A., Schubert, T., and Gerjets, P. (2017). Comparison of the Working Memory Load in N-Back and Working Memory Span Tasks by Means of EEG Frequency Band Power and P300 Amplitude. *Frontiers in Human Neuroscience*, 11. doi: 10.3389/fnhum.2017.00006.

Schmidt, R., Ruiz, M. H., Kilavik, B. E., Lundqvist, M., Starr, P. A., and Aron, A. R. (2019). Beta Oscillations in Working Memory, Executive Control of Movement and Thought, and Sensorimotor Function. *Journal of Neuroscience*, 39(42):8231–8238. doi: 10.1523/JNEUROSCI.1163-19.2019. Publisher: Society for Neuroscience Section: Symposium and Mini-Symposium.

Thuwal, K., Banerjee, A., and Roy, D. (2021). Aperiodic and Periodic Components of Ongoing Oscillatory Brain Dynamics Link Distinct Functional Aspects of Cognition across Adult Lifespan. *eneuro*, 8(5):ENEURO.0224–21.2021. doi: 10.1523/ENEURO.0224-21.2021.

Tort, A. B. L., Komorowski, R., Eichenbaum, H., and Kopell, N. (2010). Measuring Phase-Amplitude Coupling Between Neuronal Oscillations of Different Frequencies. *Journal of Neurophysiology*, 104(2):1195–1210. doi: 10.1152/jn.00106.2010.

Tseng, Y.-L., Liu, H.-H., Liou, M., Tsai, A. C., Chien, V. S. C., Shyu, S.-T., and Yang, Z.-S. (2019). Lingering Sound: Event-Related Phase-Amplitude Coupling and Phase-Locking in Fronto-Temporo-Parietal Functional Networks During Memory Retrieval of Music Melodies. *Frontiers in Human Neuroscience*, 13:150. doi: 10.3389/fnhum.2019.00150.

Van Der Meij, R., Kahana, M., and Maris, E. (2012). Phase–Amplitude Coupling in Human Electrocorticography Is Spatially Distributed and Phase Diverse. *The Journal of Neuroscience*, 32(1):111–123. doi: 10.1523/JNEUROSCI.4816-11.2012.

Van Ede, F. and Maris, E. (2016). Physiological Plausibility Can Increase Reproducibility in Cognitive Neuroscience. *Trends in Cognitive Sciences*, 20(8):567–569. doi: 10.1016/j.tics.2016.05.006.

Virtue-Griffiths, S., Fornito, A., Thompson, S., Biabani, M., Tiego, J., Thapa, T., and Rogasch, N. C. Task-related changes in aperiodic activity are related to visual working memory capacity independent of event-related potentials and alpha oscillations. preprint, Neuroscience, (2022). URL http://biorxiv.org/lookup/doi/10.1101/2022.01.18.476852.

Vogels, T. and Abbott, L. (2009). Gating Multiple Signals through Detailed Balance of Excitation and Inhibition in Spiking Networks. *Nature neuroscience*, 12(4):483–491. doi: 10.1038/nn.2276.

Voytek, B., Kramer, M. A., Case, J., Lepage, K. Q., Tempesta, Z. R., Knight, R. T., and Gazzaley, A. (2015). Age-Related Changes in 1/f Neural Electrophysiological Noise. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 35(38): 13257–13265. doi: 10.1523/JNEUROSCI.2332-14.2015.

Wager, T. D. and Smith, E. E. (2003). Neuroimaging studies of working memory:. *Cognitive, Affective, & Behavioral Neuroscience*, 3(4):255–274. doi: 10.3758/CABN.3.4.255.

Waschke, L., Donoghue, T., Fiedler, L., Smith, S., Garrett, D. D., Voytek, B., and Obleser, J. (2021). Modality-specific tracking of attention and sensory statistics in the human electrophysiological spectral exponent. *eLife*, 10:e70068. doi: 10.7554/eLife.70068.

Supplementary Information

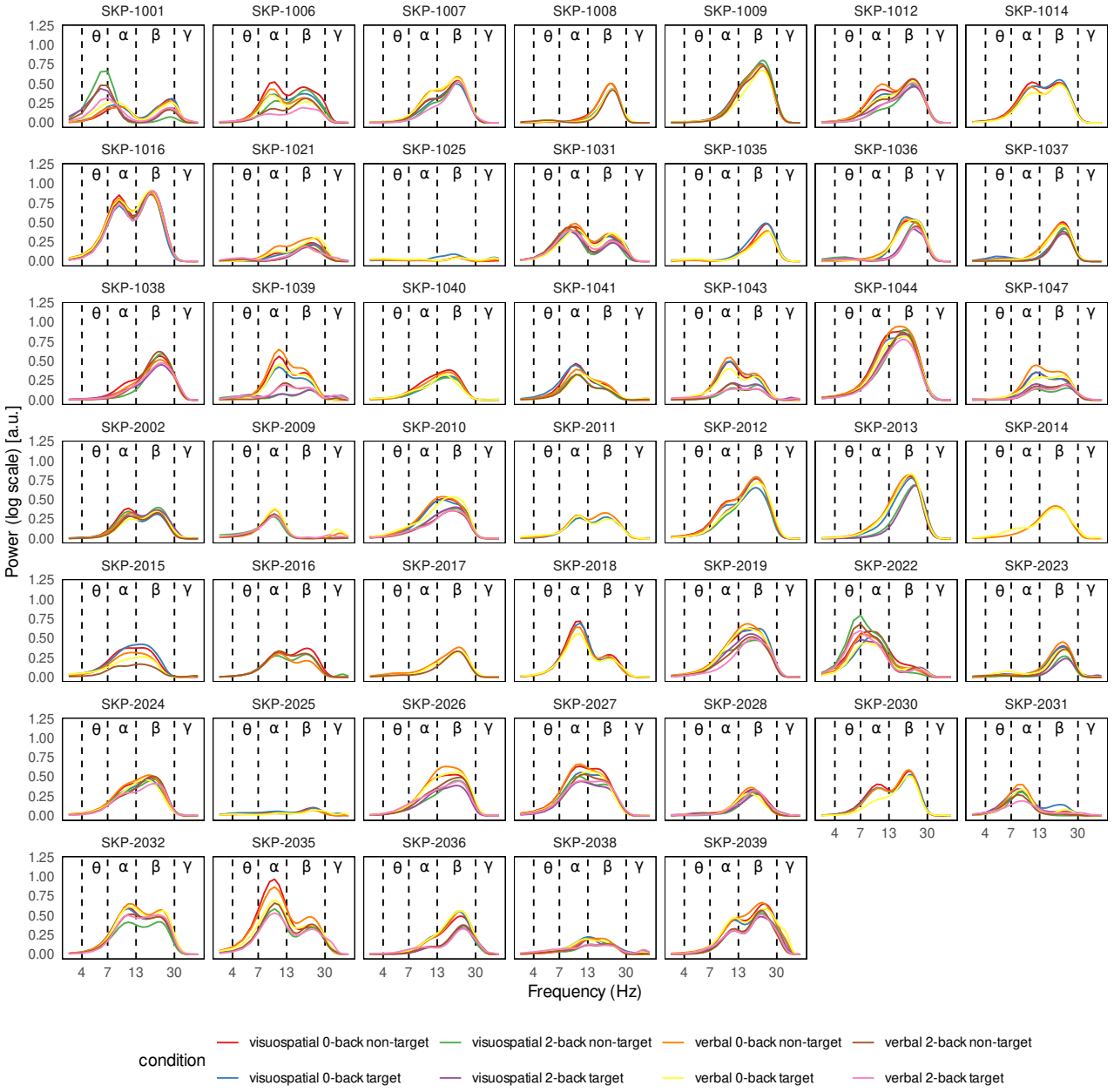

Figure S1. Power spectra of periodic activity on the Fz channel for each participant, averaged over time. Inspection of the individual periodic power spectra showed that only two participants, SKP-1001 and SKP-2022, exhibited periodic activity in the theta band. Both axes of the spectra are displayed on a logarithmic scale.

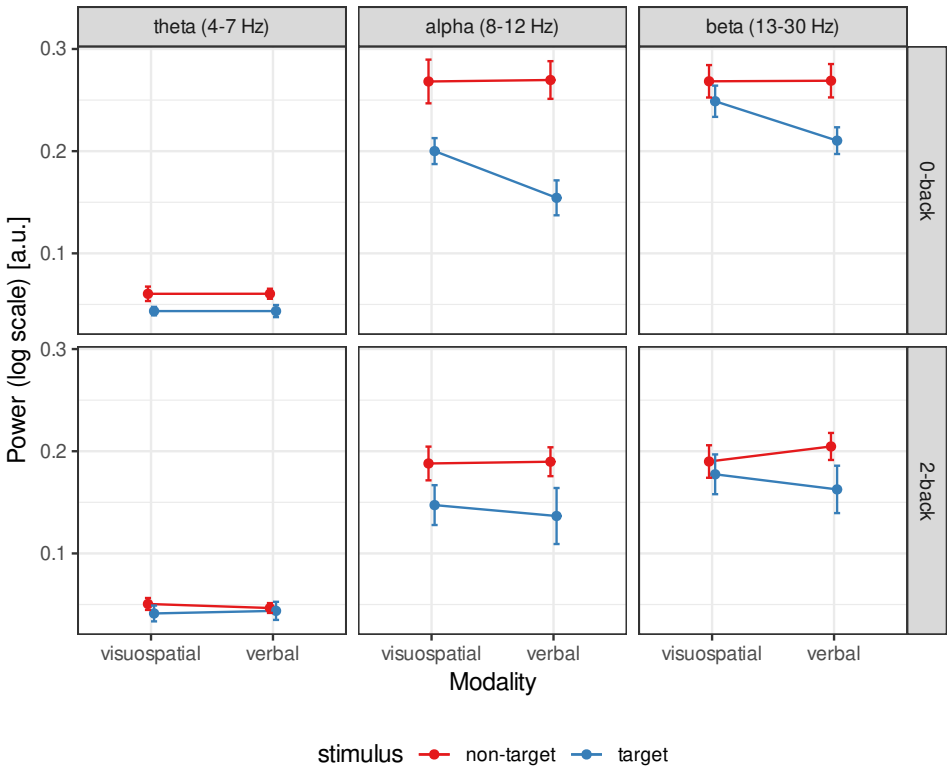

Figure S2. Power of periodic activity 0.5 to 1 second post-stimulus, averaged across all channels and participants. This visualisation facilitates the interpretation of the interaction between stimulus type and modality. It illustrates that the difference in power between target and non-target stimuli is more pronounced in the verbal task than in the visuospatial task. Error bars represent 95% Cousineau-Morey (within-subject) confidence intervals (Cousineau, 2017).

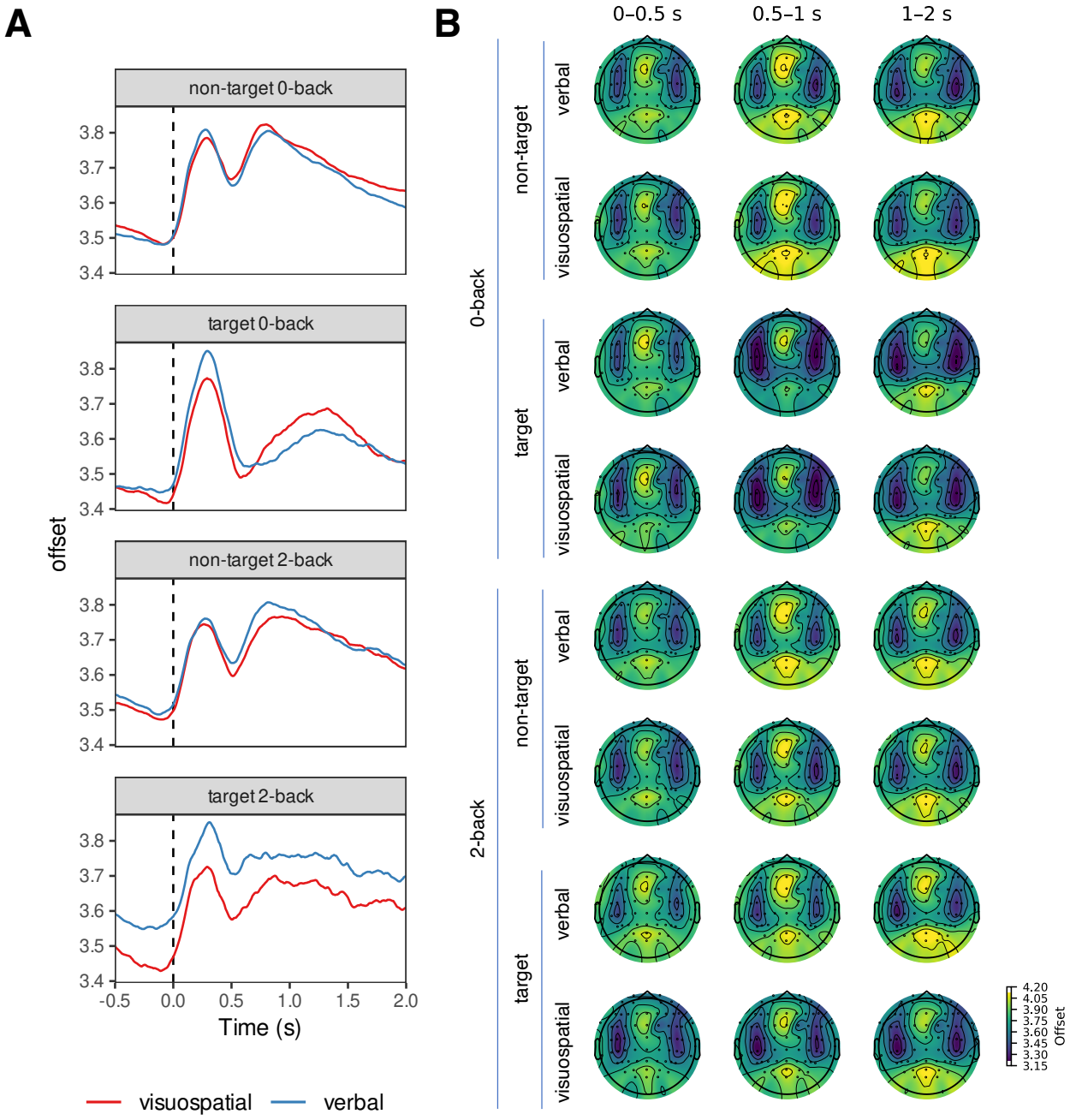

Figure S3. Temporal changes in aperiodic activity (offset).
A) As with the exponent parameter, a frontal and a parietal aperiodic component were identified, demonstrating similar spatial distributions (Figure 6).

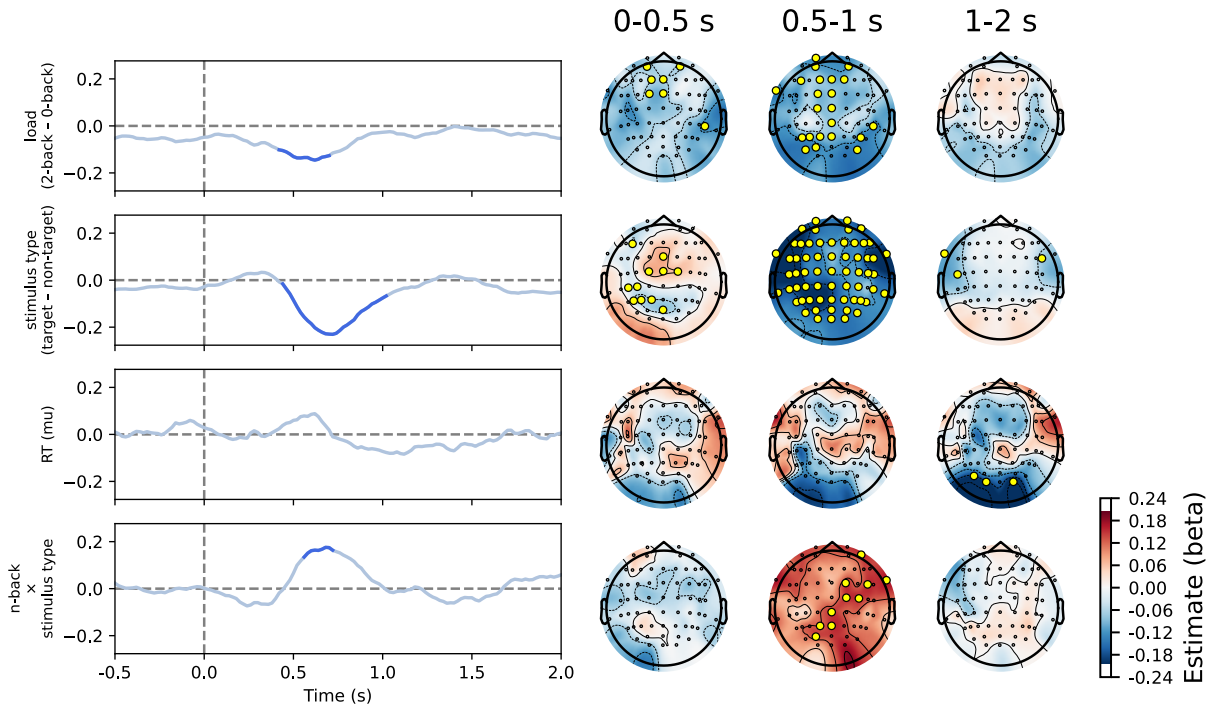

Figure S4. Results of the linear mixed model on aperiodic activity (offset parameter) of the comparison between conditions.

Significant values are shown in blue on line plots and marked with yellow circles on topographies. Results were similar to the exponent parameter (Figure 7), but there was also an effect of load at about 0.6 seconds post-stimulus.

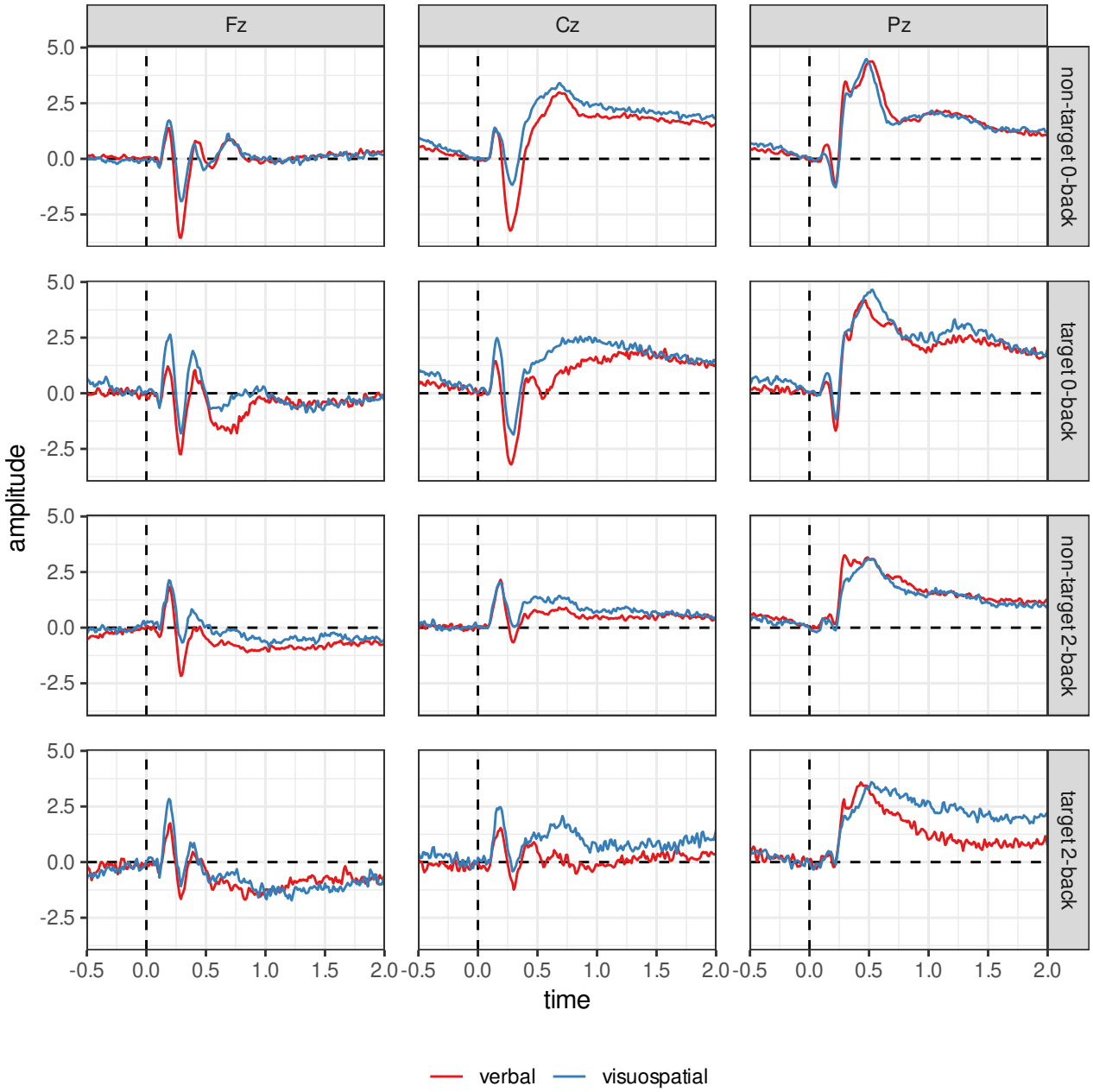

Figure S5. Grand average event-related potentials (ERPs) on midline electrodes.
ERPs have been low-pass filtered at a 40 Hz cut-off for visualisation.

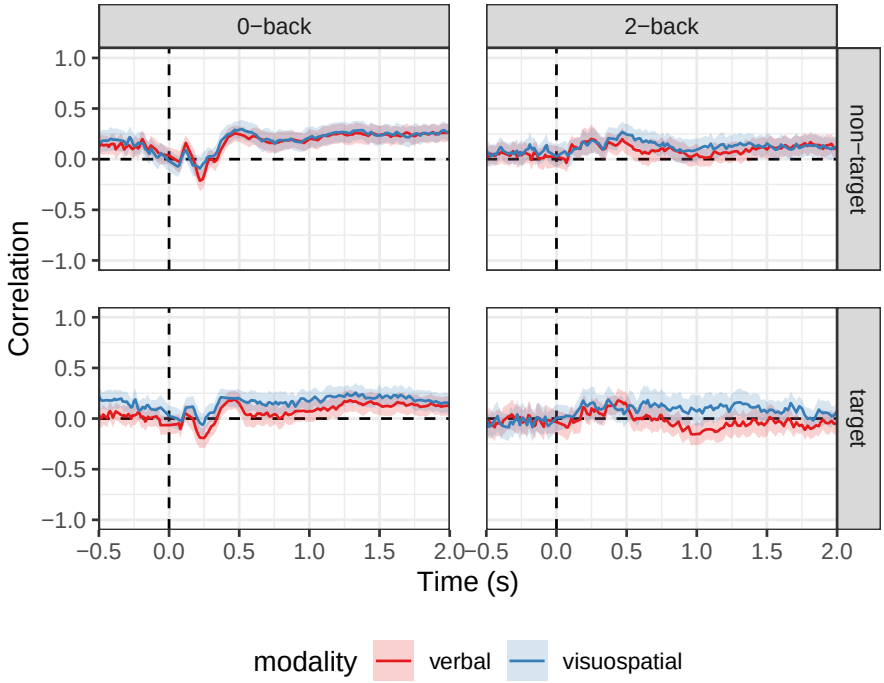

Figure S6. Correlations between ERPs and aperiodic activity (exponent).
The line represents the mean correlation across subjects and the shaded area represents the interquartile range.

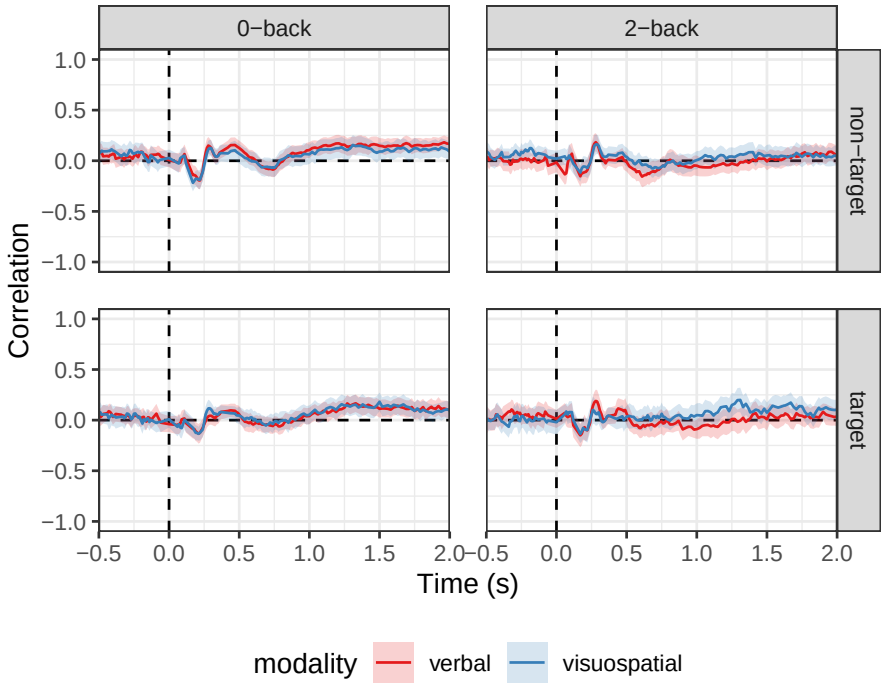

Figure S7. Correlations between ERPs and aperiodic activity (offset).
The line represents the mean correlation across subjects and the shaded area represents the interquartile range.

Control analysis

All analyses were repeated on an alternative n-back EEG dataset (Nakuci et al., 2023) and are presented here.

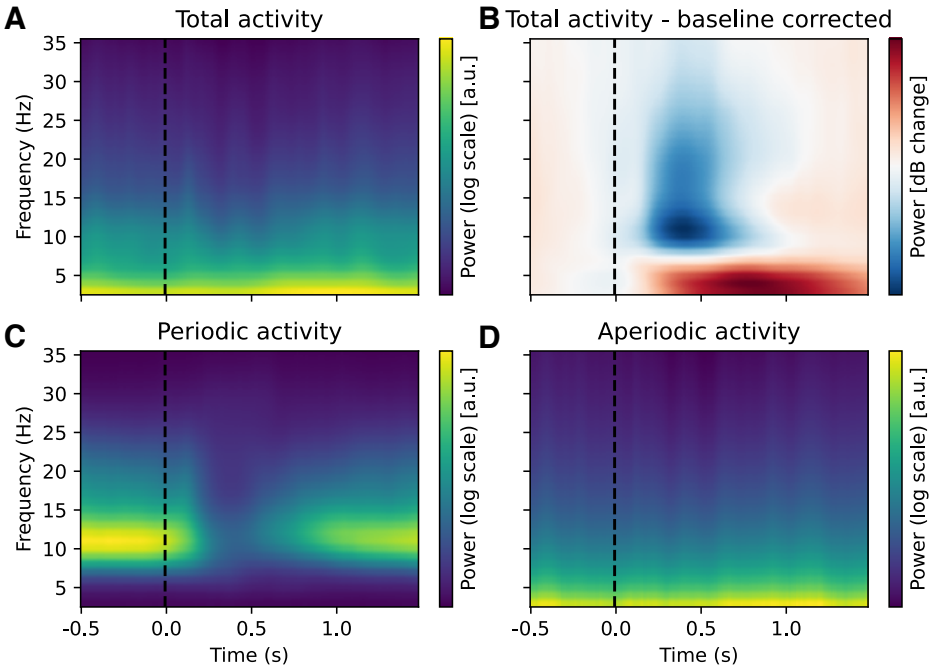

Figure S8. Effect of baseline correction and FOOOF decomposition on time-frequency decomposition (control dataset). As in the main analysis (Figure 3), baseline correction (**B**) revealed changes in alpha, beta and theta power after stimulus presentation. FOOOF decomposition showed that changes in alpha and beta were periodic (**C**), whereas changes in theta power reflected task-related changes in aperiodic activity (**D**) (see also Figure S12, Figure S14).

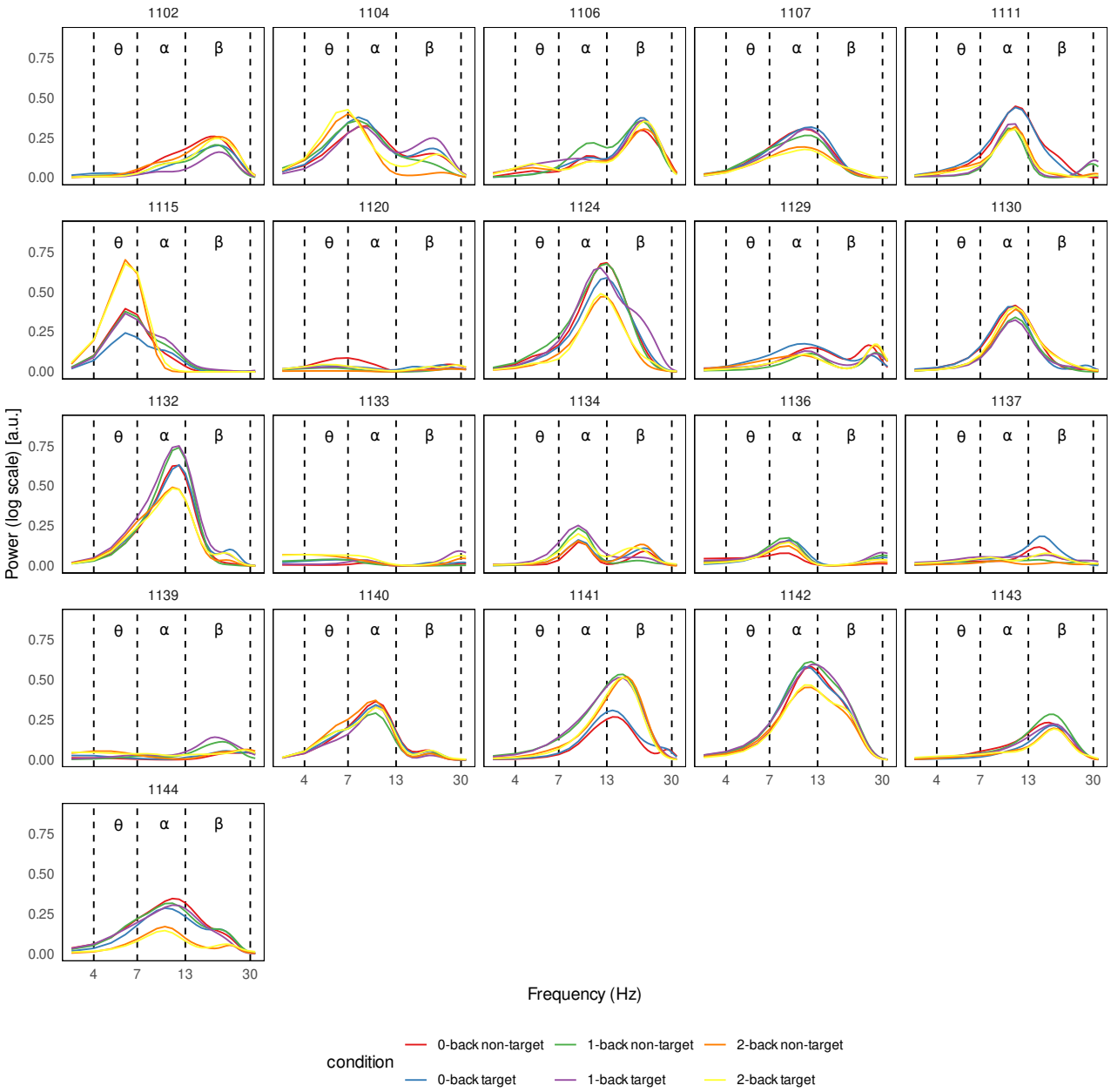

Figure S9. Power spectra of periodic activity on the E15 channel for each participant, averaged over time (control dataset).

Similar to our main analysis (Figure S1), theta periodic activity was reliably present in only one participant (1115), with another participant (1104) showing a peak at 7-8 Hz. Both axes are displayed on a logarithmic scale.

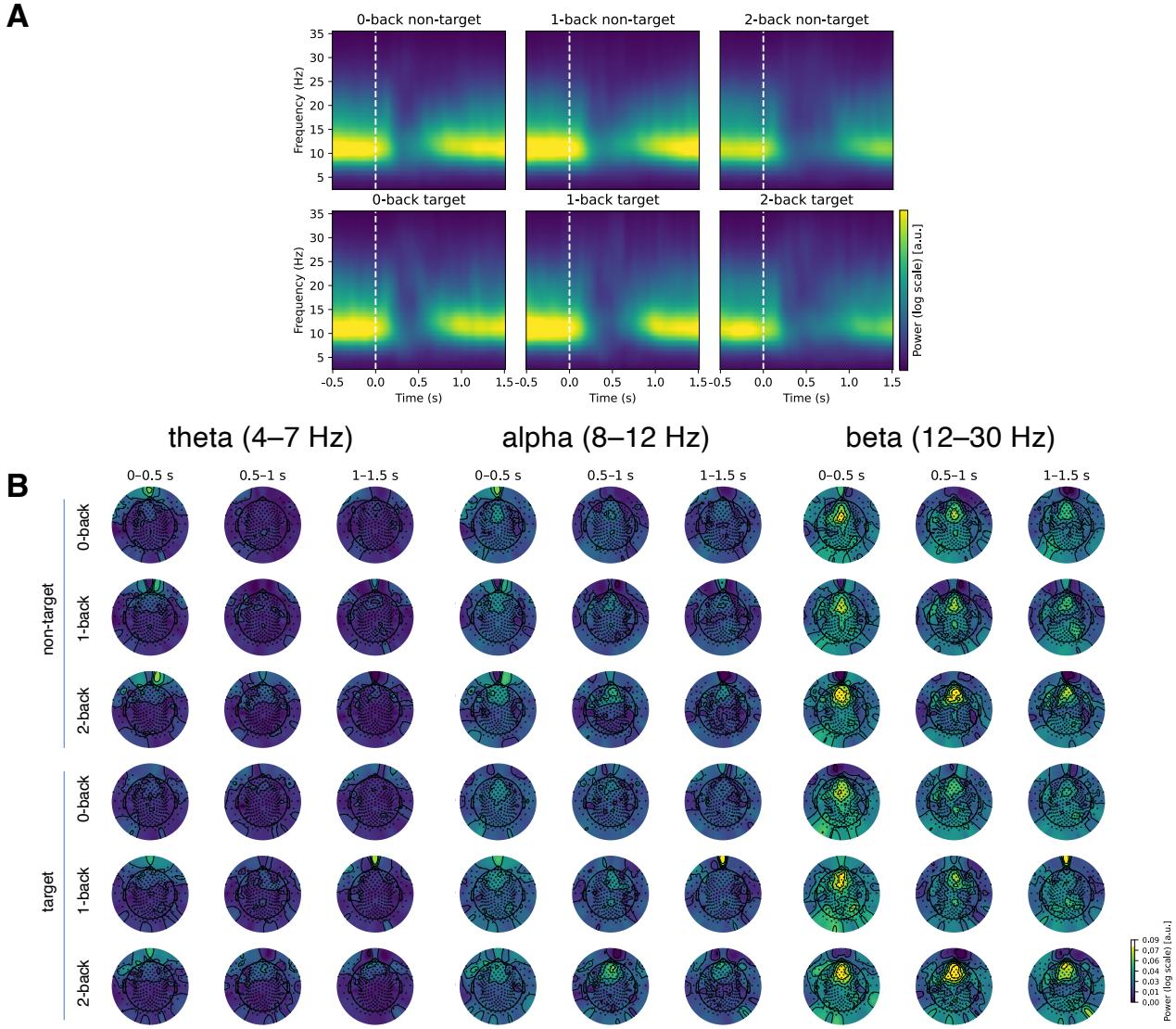

Figure S10. Changes in periodic (oscillatory) activity as a function of time (control data).
(**A**) Time course of periodic activity averaged accross all channels. The periodic activity was most pronounced in the alpha band, with a strong decrease after stimulus onset. (**B**) Alpha and beta activity was most prominent in frontal channels.

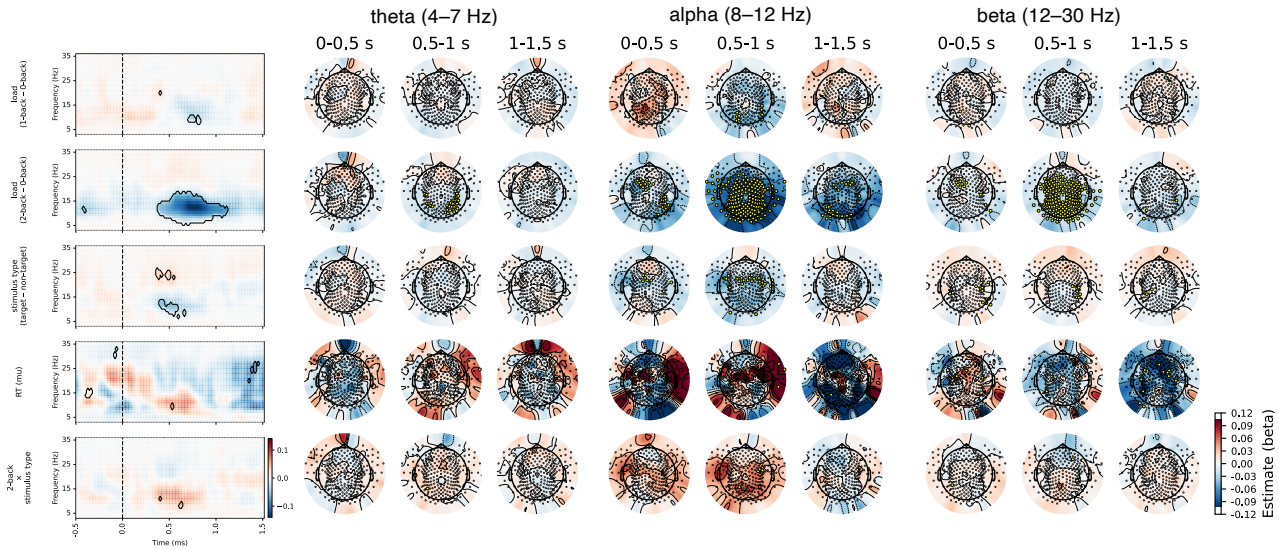

Figure S11. Results of linear mixed model on periodic activity for comparison between conditions (control data). There was a significant effect of load with reduced alpha and beta power at higher loads.

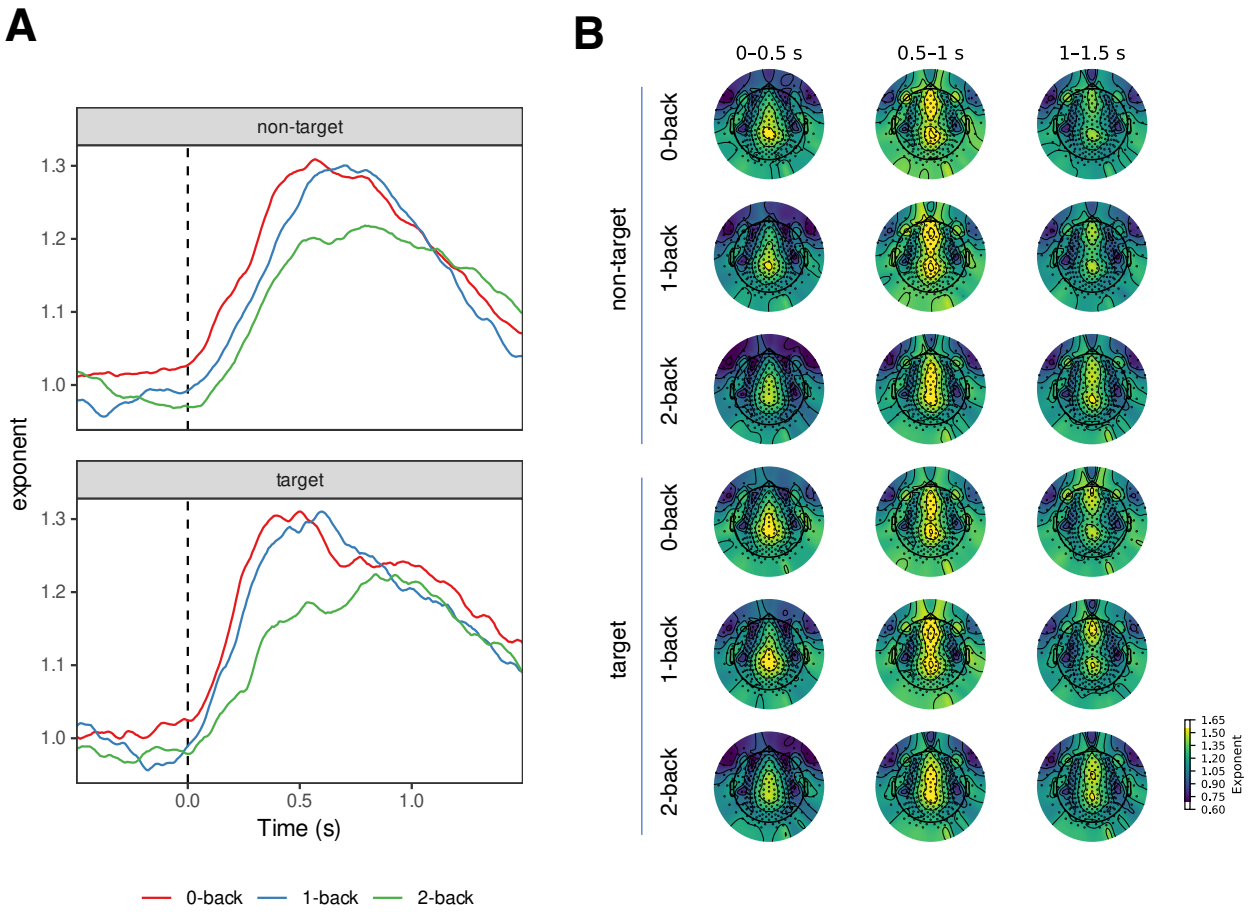

Figure S12. Changes in aperiodic activity (exponent) as a function of time (control data). Similar to the main analysis (Figure 6), we observed two peaks, early frontal and late parietal components.

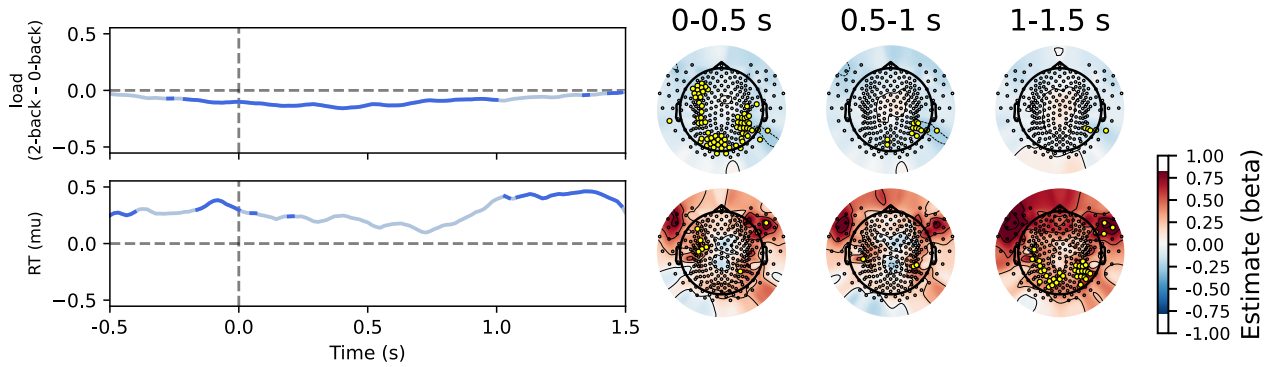

Figure S13. Results of linear mixed model on aperiodic activity (exponent) for comparison between conditions (control data).
There was a significant effect of load, most evident immediately after stimulus presentation. There was also an association with reaction times, particularly after 1 second post-stimulus.

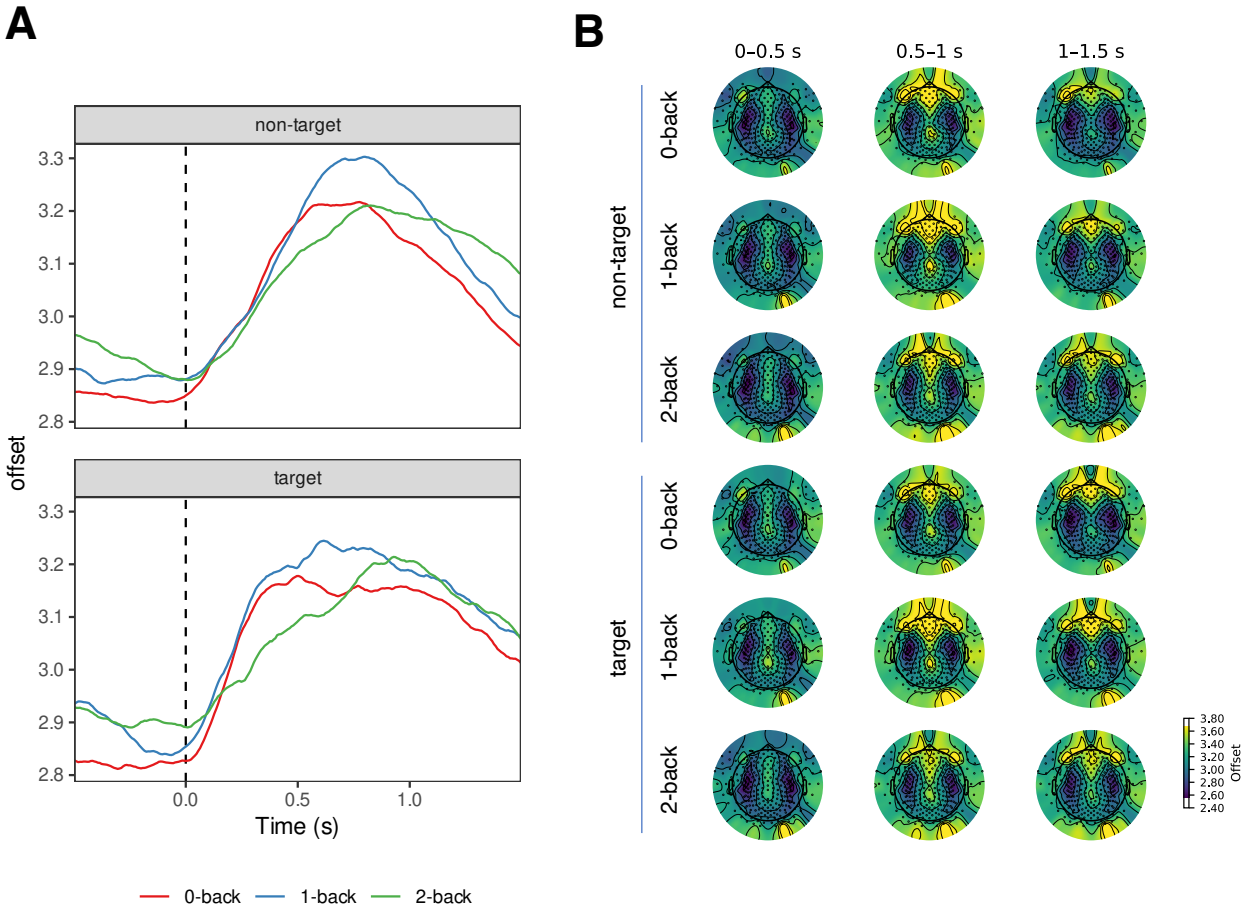

Figure S14. Changes in aperiodic activity (offset) as a function of time (control data).

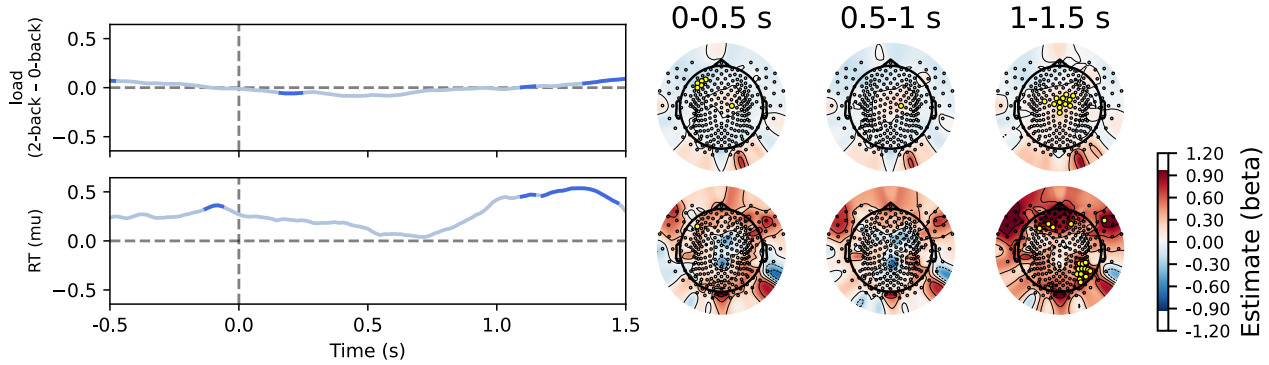

Figure S15. Results of linear mixed model on aperiodic activity (slope) for comparison between conditions (control data).

References

Cousineau, D. (2017). Varieties of Confidence Intervals. *Advances in Cognitive Psychology*, 13(2):140–155. doi: 10.5709/acp-0214-z.

Nakuci, J., Covey, T. J., Shucard, J. L., Shucard, D. W., and Muldoon, S. F. (2023). Single trial variability in neural activity during a working memory task reveals multiple distinct information processing sequences. *NeuroImage*, 269:119895. doi: 10.1016/j.neuroimage.2023.119895.