Spectral slope and neural complexity as robust markers of task demand and brain state during sleep and wakefulness

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Abstract

Spectral slope and neural complexity are affected in many neurophysiological disorders such as ADHD, autism or epilepsy and are modulated by sleep, anesthesia, and aging. Yet, these two parameters are rarely studied in relation to each other. Here, we evaluated the effects of sleep stage and task demands on spectral slope and neural complexity within a narrow- (30 – 45Hz) and broadband (3 – 45Hz) frequency range in 28 healthy male adults (21.54 ± 1.90 years) over three consecutive recordings with a set of tasks (resting, attention and memory). We show that the slope steepens, and complexity decreases from wakefulness to N3. Importantly, slope and complexity are not only modulated by sleep but also differ between tasks, with flatter slopes and higher complexity being associated with more demanding tasks. While the slope and complexity are strongly correlated within 3 – 45Hz, we observe a functional dissociation in the 30 – 45Hz range. Critically, only the narrowband slope is steepest during REM sleep and associated with better task performance in a Go/Nogo task. Our results demonstrate that both markers are powerful indices of sleep depth, task demand and cognitive performance. However, depending on the frequency range, they provide distinct information about the underlying brain state.

Introduction

To date, neural oscillations are still the most prominent electrophysiological signature of human brain activity. For instance, wakeful resting is typically characterized by pronounced alpha-band activity (8 – 12Hz), which is suppressed in active task engagement (Kirstein, 2007; Klimesch et al., 1993; Klimesch, 1999). During sleep, different stages are best described by characteristic oscillatory events like sleep spindles and slow oscillations (Davis et al., 1938; Richard et al., 2012; Terzano et al., 2002). However, recent evidence suggests that irregular and aperiodic brain activity by means of neural complexity (Lempel & Ziv, 1976 and Welch, 1984) and the spectral exponent *ß* (i.e., the magnitude of decay in power with increasing frequency; He, 2014), also carries meaningful information about different brain states. Specifically, the spectral exponent has been discussed as a marker of the brain's excitation and inhibition (E/I) balance (Gao et al., 2017), which is impaired in a variety of clinical conditions such as the attention deficit hyperactivity disorder (ADHD, Karalunas et al., 2022; Robertson et al., 2019), autism (Gao & Penzes, 2015; Rubenstein & Merzenich, 2003) and epilepsy (Symonds, 1959; Wong, 2010). In addition, epilepsy has further been associated with alterations in neural complexity (Aarabi & He, 2012; Zhu et al., 2017).

Conceptually, the spectral exponent and neural complexity are regarded as two distinct measures as they are derived by different analytical approaches from the underlying electrophysiological signal. Neural complexity computed as Lempel-Ziv-Welch complexity (Welch, 1984) expresses the regularity and compressibility of a signal in time-domain (Lau et al., 2022) and is thought to be still strongly influenced by oscillatory activity (González et al., 2022; Tosun et al., 2019). In contrast, the spectral exponent reflects the absolute value of the slope (i.e., steepness) of a signal's power spectrum in frequency-domain, which is thought to be mainly aperiodic (Donoghue et al., 2020). In the following, we always use and refer to the spectral slope instead of the spectral exponent (which would be the absolute value of the slope) in order to avoid any ambiguity due to different terms that are often used to describe the same parameter (e.g., 1/f signal and scale free or aperiodic activity).

Despite the apparent differences between the spectral slope and neural complexity, the literature suggests that both can capture changes in brain states in a surprisingly similar fashion. Regarding consciousness and sleep, multiple studies showed that the spectral slope steepens (i.e., becomes more negative) during anesthesia compared to wakefulness (Colombo et al., 2019; Gao et al., 2017; Lendner et al., 2020; Waschke et al., 2021), while others showed the same pattern for neural complexity, which also decreases from wakefulness to anesthetized states (Ferenets et al., 2007; Zhang et al., 2001). This mirrors findings of the transition from wakefulness to sleep, where spectral slope (Lendner et al., 2020; Ma et al., 2018; Miskovic et al., 2019; Pereda et al., 1998) and neural complexity (Andrillon et al., 2016; Schartner et al., 2017) both decrease with increasing sleep depth (i.e., from wakefulness to N3 sleep). Besides changes in consciousness, recent evidence from Waschke et al. (2021) further suggests that the spectral slope can even track the level of attention, whereby higher levels of attention and quicker response times are indexed by flatter slopes. This is in line with findings from other studies, which showed that the slope is indicative of cognitive processing speed (Ouyang et al., 2020; Pathania et al., 2022) and modulated by cognitive decline in ageing (Dave et al., 2018; Voytek et al., 2015; Voytek & Knight, 2015). Interestingly, Mediano et al. (2020) recently showed that higher neural complexity values also relate to faster reaction times on a trial-by-trial basis, thus likewise serving as a proxy of attention or processing speed.

With respect to the influence of different frequency contents on the estimation of the spectral slope and neural complexity, no optimal frequency settings are established yet for any of the two parameters. The heterogeneity of frequency content on which the calculations of both measures are based might be responsible for some disparate results in the current literature, thus further hampering our understanding of the contribution of aperiodic brain activity to healthy brain functioning. For instance, González et al. (2022) suggest that particularly for neural complexity, lower frequencies (≤ 12Hz) are more informative than higher frequencies when differentiating between sleep and wakefulness. For the estimation of the spectral slope, researchers have argued either in favor of broadband (Karalunas et al., 2022; Podvalny et al., 2015; Waschke et al., 2021) or narrowband (Gao et al., 2017; Lendner et al., 2020) frequency ranges. While broadband ranges encompass more of the total signal power and result in better overall slope-fits (Donoghue et al., 2020; Gerster et al., 2022), narrowband ranges are less affected by low-frequency oscillatory activity and are therefore reflecting mostly pure aperiodic activity (Gao et al., 2017; Lendner et al., 2020).

Taken together, the slope and complexity research findings suggest a functional overlap of neural complexity and spectral slope in tracking different brain states. However, to date a direct comparison of these two measures across different brain states during sleep and wakefulness is still missing. Thus, the relationship between slope and complexity across different brain states still remains unclear as it has only been compared between rested wakefulness and anesthesia so far (Medel et al., 2020). Additionally, little is known about the sensitivity of the spectral slope and neural complexity to changes in brain activity during wakefulness in general. As potential markers of arousal and attention, the two parameters might likely be so affected by varying levels of task demands, which require different amounts of cognitive resources. Finally, it is unclear how the two measures are affected by selecting different frequency contents for their calculation.

Here, we leverage an expansive, within-subject design with multiple sleep and wake recordings to investigate (1) whether the spectral slope and neural complexity are modulated by different brain states during sleep and wakefulness and (2) to what extent they are related to each other as well as their functional significance for cognition. Using multiple recording sessions per subject, we try to overcome a limitation of most previous research that only relies on single session recordings, thus, limiting insights into the robustness of the observed effects. First, we assess the performance of the spectral slope and neural complexity in delineating sleep from wakefulness. Second, we investigate the influence of task demands on both measures by increasing task difficulty form simple resting sessions to an auditory attention (Go/Nogo) and a declarative memory task. Third, we analyze the relationship between the spectral slope and neural complexity across brain states and tasks using either narrow- or broadband frequency ranges for estimation. Finally, we probe whether the two parameters track behavioral performance in the Go/Nogo and declarative memory tasks.

Results

We utilized the data from a recently published study (Höhn et al., 2021; Schmid et al., 2021) that investigated the effects of different light conditions on alertness, sleep and memory consolidation. The subjects underwent the same experimental protocol on three different days under highly controlled and standardized lighting conditions. On three consecutive experimental nights, multiple tasks were conducted before and after sleep, including two resting sessions with either eyes closed or open, an auditory attention task (Go/Nogo) and a declarative memory task (cf., Figure 1A). We calculated spectral slopes and neural complexity (using Lempel-Ziv complexity) for all sleep stages and tasks in a narrow- (30 – 45Hz) and broadband (3 – 45Hz) frequency range (cf., Figure 1B and C).

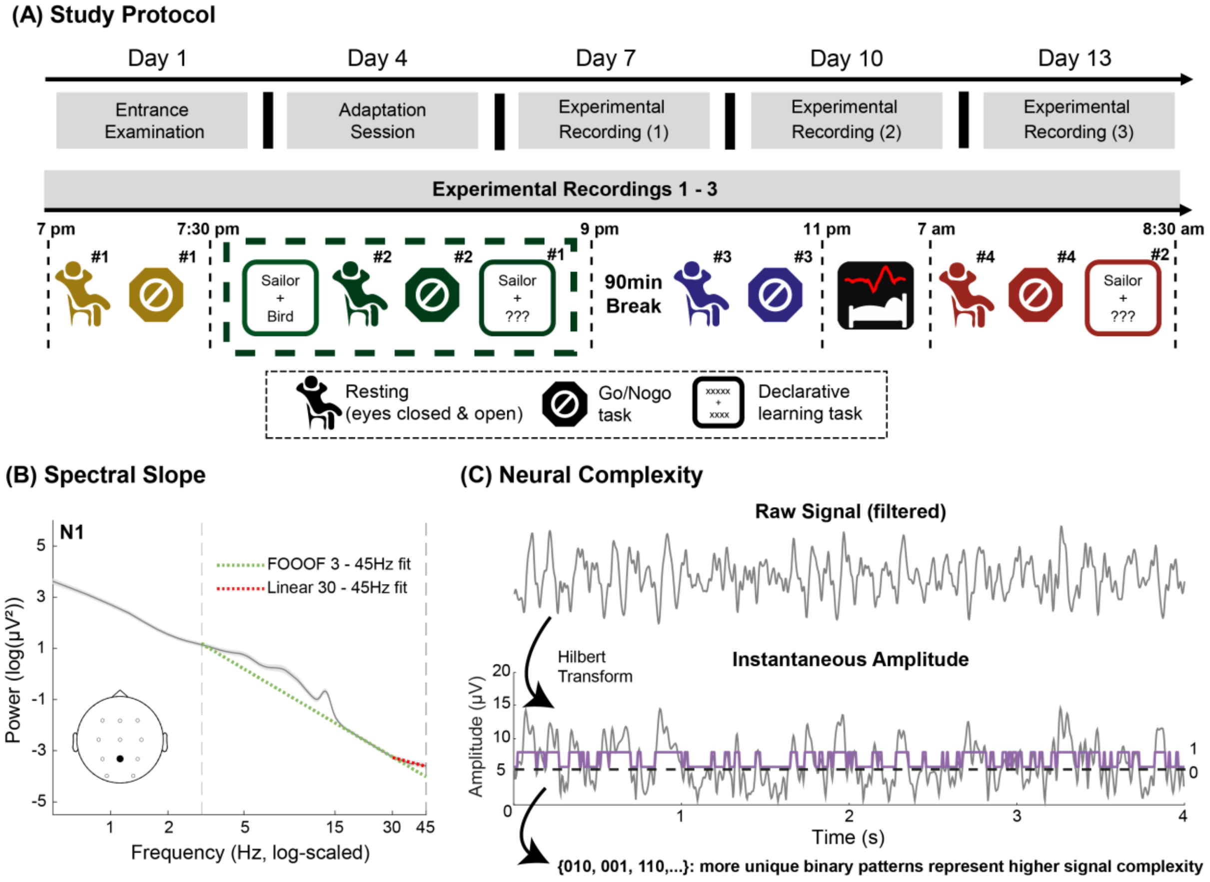

Figure 1. (A): Overview of the experimental protocol. EEG was recorded throughout all tasks and during sleep (with full-night polysomnography) on the experimental days 7, 10 and 13. The tasks, which are highlighted by a dashed, dark-green rectangle were primarily used to analyze the effects of task demand. The adaptation session only served familiarization purposes and was not considered in any of the analyses. Results from the entrance examination questionnaires are presented in Supplementary file – Table 1. (B): Example of the spectral slope estimation during N1 sleep. For illustration purposes, data is shown for the electrode Pz averaged over all subjects and sleep recordings. The spectral slope was fitted within 3 – 45Hz (broadband, dashed green line) and 30 – 45Hz (narrowband, dashed red line). (C): Schematic overview of the neural complexity calculation based on a random 4s epoch from electrode Pz of a subject during resting with closed eyes. First, the raw signal, filtered within the broad- or narrowband frequency range (in this case within the 3 – 45Hz broadband range), is Hilbert transformed. Second, the resulting data is binarized around its median amplitude and stored as a vector of zeros and ones. Lastly, the Lempel-Ziv-Welch algorithm (Welch, 1984) is applied on this binary sequence in order to obtain a neural complexity value, which is driven by the number of unique repetitions of ones and zeros.

Spectral slope and neural complexity delineate brain states during sleep

First, we strived for replicating previous findings, which showed that sleep stages could be differentiated solely based on the spectral slope and neural complexity. The effect of sleep stage was assessed for the spectral slope and neural complexity in each frequency range (30 – 45Hz and 3 – 45Hz) with semi-parametric Wald-Type Statistics (WTS; Friedrich et al., 2019) averaged over all electrodes while considering the three repeated measurements.

The narrowband (30 – 45Hz) spectral slope model (*WTS* (4) = 133.57, *p* < .001) and the neural complexity model (*WTS* (4) = 14.11, *p* = .030) both indicated significant modulations by sleep stage. In line with previous research, the narrowband slope was significantly steeper in all sleep stages compared to wakefulness with the steepest slope during REM sleep. In contrast, the narrowband neural complexity slightly increased from wake to sleep and showed a diverging pattern in comparison to the spectral slope (see Figure 2). When the broadband (3 – 45Hz) frequency range was used for estimation, the effect of sleep stage was much more pronounced in both parameters (spectral slope: *WTS* (4) = 560.01, $p < .001$; neural complexity: *WTS* (4) = 601.92, $p < .001$). Both, the broadband slope and complexity significantly decreased from shallow (N1) to deep NREM sleep (N3). For REM sleep, however, both markers increased again in remarkably similar ways (see Figure 3), arguably reflecting more wake-like brain activity in the broadband range.

We found no significant effects of the repeated measurements (all $p_{\text{adj.}} \geq .166$ after correcting for multiple comparisons), revealing that the effect of sleep stage robustly emerged in all individual recordings per subject. To evaluate the topographical distribution of the spectral slope and neural complexity, we additionally ran a multivariate pattern analysis (MVPA) with multi-class linear discriminant analyses (LDA). With this MVPA, we quantified how well the sleep stages could be decoded by taking the topographical distribution of the slope and complexity values into account. In both frequency ranges and for both parameters, classification accuracies were always significantly above chance level (20%, $p < .001$) and in general higher for the broadband (3 – 45Hz) than for the narrowband (30 – 45Hz) frequency range (*WTS* (1) = 643.36, $p < .001$). For both frequency ranges, the spectral slope was more informative about the underlying brain state (i.e., yielded higher classification accuracies) than the neural complexity (*WTS* (1) = 123.88, $p < .001$), especially in the narrowband range (spectral slope: 31.83%, neural complexity: 22.67%; see Figure 3 – Figure Supplement 1).

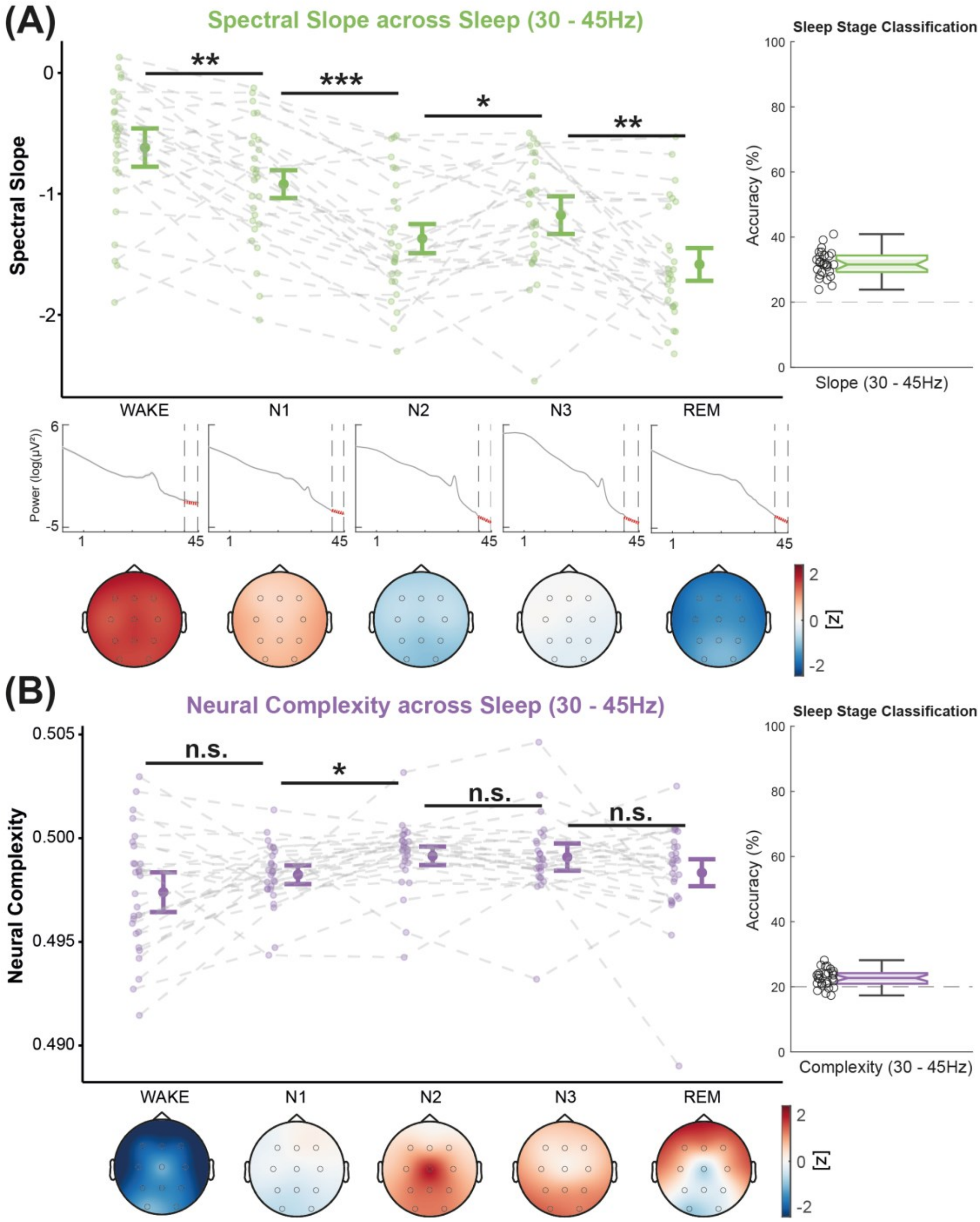

Figure 2. Spectral slope (green, A) and neural complexity (purple, B) from 30 – 45Hz across sleep, averaged over all lab-sessions per subject. Center figures show the data averaged over all electrodes and topographical maps are provided below (color-coding refers to z-values of slope or complexity computed from the grand average across all sleep stages). In (A), the power spectra in log-log space are provided for each sleep stage to illustrate the narrowband slope changes across different sleep stages. Classification accuracies are shown on the right-hand side. A: The spectral slope decreases from wakefulness across all sleep stages to REM sleep with a small temporary increase during N3 sleep. B: Neural complexity increases from shallow N1 to light N2 sleep and is in general less modulated by sleep stages than the spectral slope. ***: $p < .001$, **: $p \leq .010$, *: $p \leq .050$, n.s.: $p > .050$; all p-values are adjusted for multiple comparisons; error-bars represent 95% confidence intervals ($N = 27$).

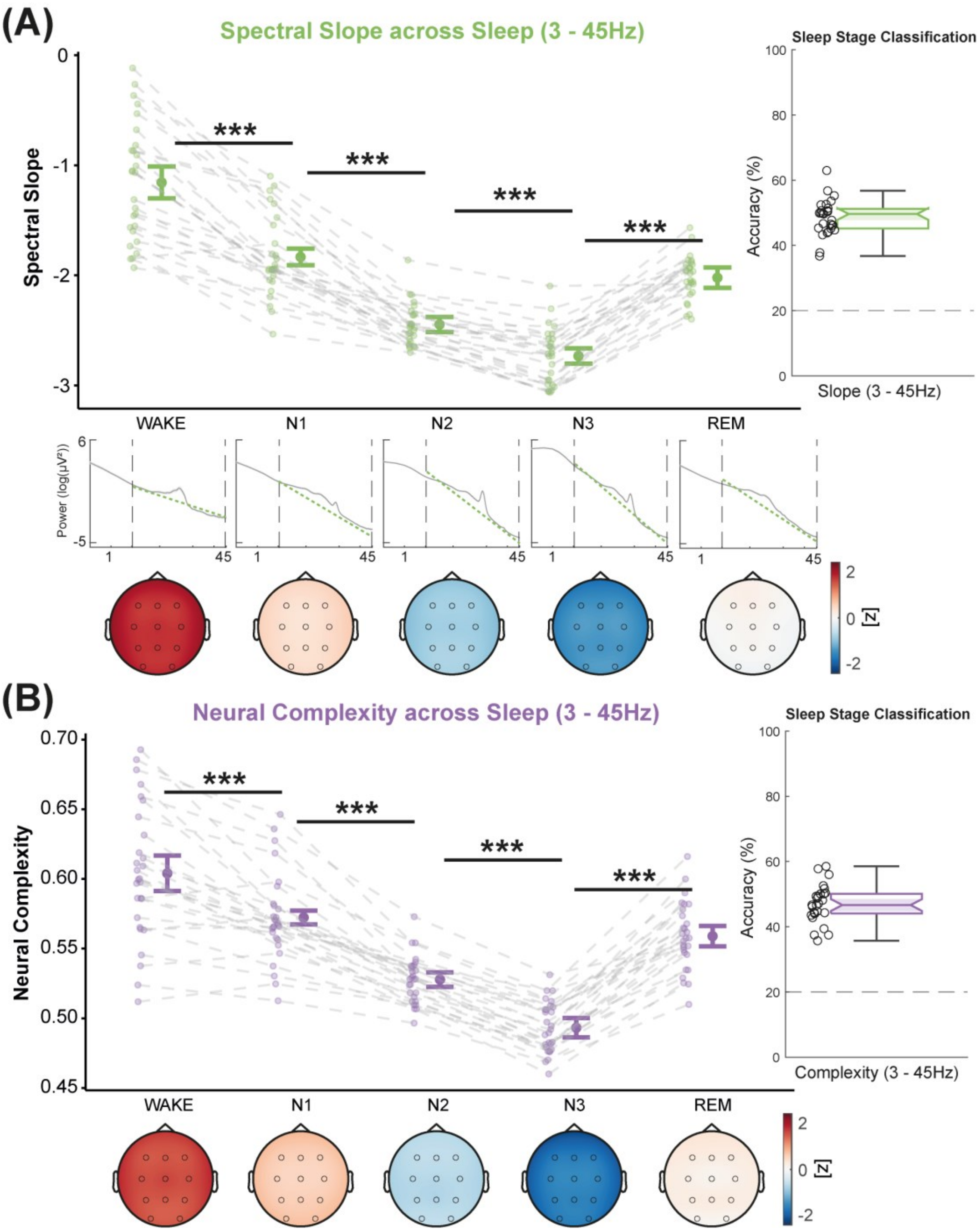

Figure 3. Spectral slope (green, A) and neural complexity (purple, B) from 3 – 45Hz across sleep, averaged over all lab-sessions per subject. Center figures show the data averaged over all electrodes and topographical maps are provided below (color-coding refers to z-values of slope or complexity computed from the grand average across all sleep stages). In (A), the log-log power spectra for each sleep stage are provided to illustrate the broadband slope differences across sleep stages. Classification accuracies are shown on the right-hand side. (A): Spectral slope steepens from wakefulness to N3 sleep but flattens to some extent during REM sleep. (B): Neural complexity shows the same pattern as the spectral slope and likewise decreases from wakefulness to N3 with a subsequent increase in REM sleep. ***: $p < .001$, **: $p \leq .010$, *: $p \leq .050$, n.s.: $p > .050$; p-values are adjusted for multiple comparisons; error-bars represent 95% confidence intervals ($N = 27$).

Figure 3: Supplement 1. Direct comparison of the classification accuracies across sleep between neural complexity and spectral slope for the narrow- (30 – 45Hz) and broadband (3 – 45Hz) frequency ranges.

Spectral slope and neural complexity vary as a function of task demand

Next, we investigated whether spectral slope and neural complexity track varying levels of task demand. We calculated both markers from resting sessions with eyes closed (REC) and eyes open (REO), an auditory Go/Nogo task (GNG), an encoding session (ENC) from a declarative memory task as well as its according retrieval session (RET). For these analyses, we focused on the task data from the evening recordings (see dashed dark-green rectangle in Figure 1A). Theoretically, task demands should have been comparable between resting sessions with closed and open eyes, whereas the Go/Nogo and encoding tasks were considered to be more demanding since they required active task participation and higher cognitive control. The retrieval task was deemed to be the most challenging as it was necessary to make an additional active memory recall as quickly as possible.

In the narrowband frequency range (30 – 45Hz), we observed a significant flattening (i.e., values closer to zero) of the slope (*WTS* (4) = 56.64, $p < .001$) but a decrease in complexity (*WTS* (4) = 199.55, $p < .001$) with increasing task demands (see Figure 4). The flattening of the narrowband spectral slope was most pronounced when contrasting resting states with the Go/Nogo (REC vs. GNG: *WTS* (1) = 21.05, $p_{adj.} < .001$; REO vs. GNG: *WTS* (1) = 16.53, $p_{adj.} = .001$) and encoding (REC vs. ENC: *WTS* (1) = 20.73, $p_{adj.} < .001$; REO vs. ENC: *WTS* (1) = 15.56, $p_{adj.} = .001$) sessions. However, further flattening of the slope was observable during the retrieval task (GNG vs. RET: *WTS* (1) = 6.44, $p_{adj.} = .021$; ENC vs. RET: *WTS* (1) = 13.66, $p_{adj.} = .001$). The narrowband neural complexity did not differ between the resting and Go/Nogo sessions (all $p_{adj.} > .110$) but decreased from the Go/Nogo to the encoding session (GNG vs. ENC: *WTS* (1) = 16.64, $p_{\text{adj.}} < .001$) and was lowest during retrieval (GNG vs. RET: *WTS* (1) = 98.74, $p_{\text{adj.}} < .001$, ENC vs. RET: *WTS* (1) = 31.11, $p_{\text{adj.}} < .001$).

When investigating the broadband frequency range (3 – 45Hz), we found that the diverging pattern between spectral slope and neural complexity disappeared and both parameters were increasing (i.e., higher complexity values and flatter slopes indexed by less negative values) across tasks (Slope: *WTS* (4) = 101.04, $p < .001$; Complexity: *WTS* (4) = 80.28, $p < .001$; see Figure 5). In the broadband frequency range, neural complexity also differed between the two resting sessions (eyes closed and eyes open), likely reflecting a difference in alpha power (8 – 12Hz) between the two conditions, thus supporting a greater influence of oscillations on estimates of neural complexity. Again, we did not observe any effects of the repeated measurements (all $p_{\text{adj.}} \geq .252$).

During wakefulness, the MVPA results indicated an above chance classification performance for all tasks (20%, $p < .001$). Similar to the results during sleep, classification accuracy was higher when using the broadband instead of the narrowband frequency range (*WTS* (1) = 397.08, $p < .001$). The spectral slope was again more informative in the narrowband range (Slope: 35.03%, Complexity: 25.98%, *WTS* (1) = 71.93, $p < .001$) while the complexity yielded better results in the broadband range (Slope: 48.10%, Complexity: 52.69%, *WTS* (1) = 13.61, $p = .002$; see Figure 5 – Figure Supplement 1).

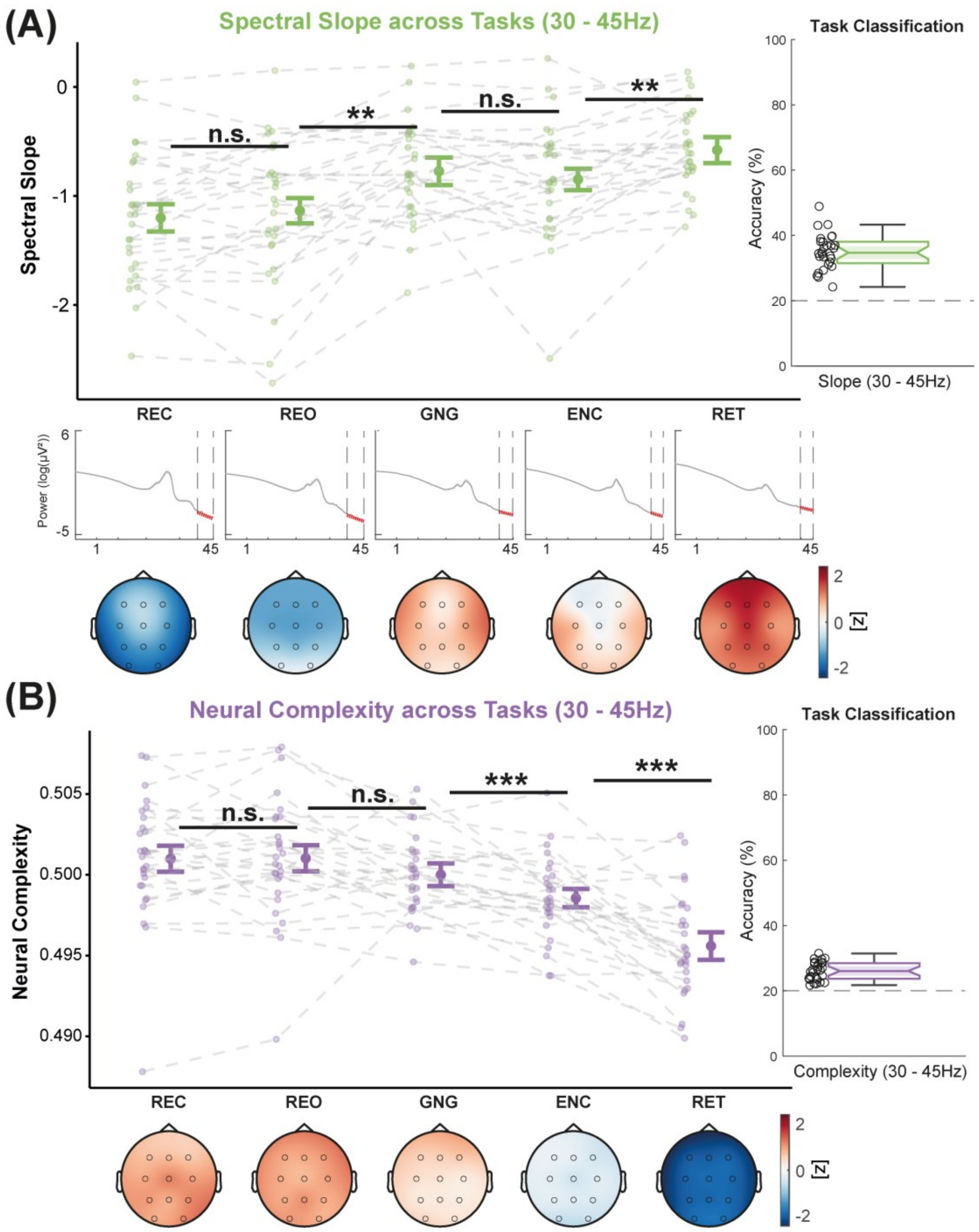

Figure 4. Spectral slope (green, A) and neural complexity (purple, B) from 30 – 45Hz across tasks, averaged over all lab-sessions per subject. Center figures show the data averaged over all channels and topographical maps are provided below (color-coding refers to z-values of slope or complexity computed from the grand average across all tasks). In (A), the log-log power spectra for each task are provided to illustrate narrowband slope differences across tasks. Classification accuracies are shown on the right-hand side. (A): The slope flattens with increasing task demands but does not differ between the resting or the Go/Nogo and encoding sessions. (B): Neural complexity decreases across tasks and is minimal during the retrieval session. ***: $p < .001$, **: $p \leq .010$, *: $p \leq .050$, n.s.: $p > .050$; p-values adjusted for multiple comparisons; error-bars show 95% confidence intervals ($N = 28$).

Figure 4: Supplement 1. Slope and complexity from 30 – 45Hz across tasks averaged over all timepoints.

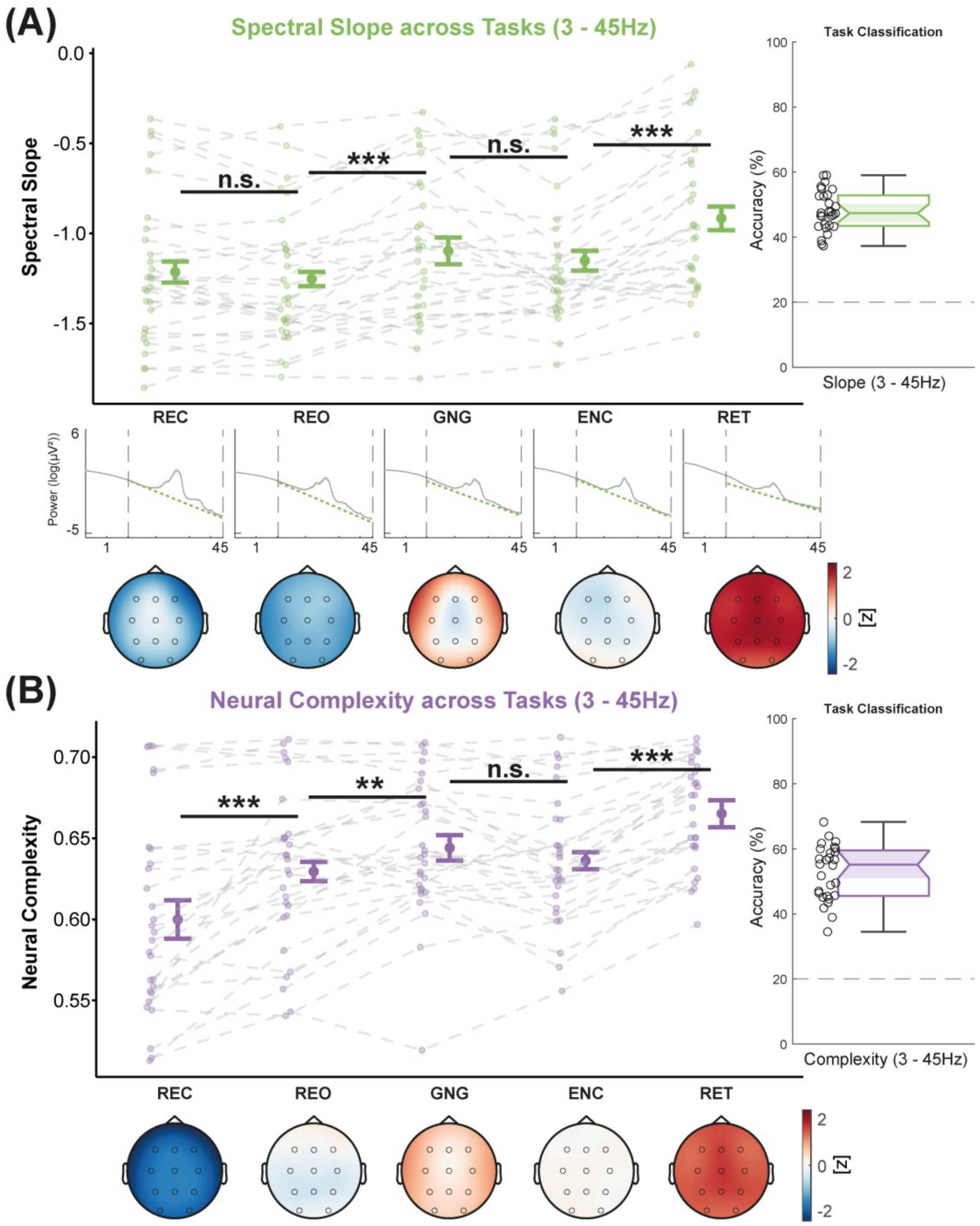

Figure 5. Spectral slope (green, A) and neural complexity (purple, B) from 3 – 45Hz across tasks, averaged over all lab-sessions per subject. Center figures show the data over all channels and topographical maps are provided below (color-coding refers to z-values of slope or complexity computed from the grand average over all tasks). In (A), the log-log power spectra for each sleep stage are provided to illustrate broadband slope differences across tasks. Classification accuracies are shown on the right-hand side. (A): The slope flattens from the resting to the Go/Nogo sessions and is flattest during retrieval. (B): Neural complexity increases already from resting with closed to open eyes and is further elevated in all active tasks, peaking during retrieval. ***: $p < .001$, **: $p \leq .010$, *: $p \leq .050$, n.s.: $p > .050$; p-values adjusted for multiple comparisons; error-bars show 95% confidence intervals ($N = 28$).

Figure 5: Supplement 1. Comparison of the classification accuracies across tasks between neural complexity and spectral slope for the narrow- (30 – 45Hz) and broadband (3 – 45Hz) frequency ranges.

Figure 5: Supplement 2. Slope and complexity from 3 – 45Hz across tasks averaged over all timepoints.

Figure 5: Supplement 3. Spectral slope and neural complexity between tasks after correcting for the resting eyes open condition as baseline.

To control whether the results were confounded by the task order and thus solely reflect an increase in exhaustion or decrease in motivation, we repeated the analyses with the task data averaged over all available time points (cf., Figure 1A for all time points at which each task was conducted). These control analyses confirmed the same patterns as in the original analyses with a very similar flattening of the broad- and narrowband spectral slopes across tasks and an increase in broadband but a decrease in narrowband complexity with increasing task demands (see Figure 4 – Figure Supplement 1 and Figure 5 – Figure Supplement 2).

An overview of the pairwise classification accuracies for all sleep stage and task pairings is presented in Supplementary file – Tables 2 and 3. All tasks and sleep stages could be differentiated above chance-level (50% in this context). As described above, the classification accuracy was in general higher for the broadband than the narrowband frequency range. However, in the narrowband frequency range, the accuracies for the spectral slope were consistently higher than for neural complexity.

Collectively, the results so far suggest that spectral slope and neural complexity are both sensitive markers, which can track brain state changes during sleep and wakefulness due to changes in sleep depth or because of varying levels of task demand and cognitive load. However, while the two parameters are modulated in remarkably similar ways when using a broadband frequency range (3 – 45Hz), they express diverging patterns when a restricted narrowband frequency range (30 – 45Hz) is used. Therefore, we next assessed the relationship between spectral slope and neural complexity.

Relationship between the spectral slope and neural complexity

First of all, we assessed the robustness of the spectral slope and neural complexity estimations over the different recordings per subject. We correlated each parameter (in the narrow- and broadband frequency range) with itself between the different lab-sessions for each sleep stage and task. Between all lab-sessions, the parameters were strongly positively correlated, indicating a substantial overlap of information over the different recordings (see Supplementary file - Table 4). To identify the relationship between the spectral slope and neural complexity for each of the two frequency ranges, we further computed the correlations between the two parameters. In the broadband frequency range, the slope and complexity were consistently positively correlated across all sleep stages and tasks (see Figure 6A and B, right columns). However, this relationship vanished in the narrowband frequency range where the correlations between the two parameters were inconsistent and ranged from significant negative to positive ones (see Figure 6A and B, left columns). These results imply that the two parameters do not share a lot of information in the narrowband range. In contrast, the information is almost entirely redundant in the broadband frequency range. This fits well to our previous results (cf., Figures 2 – 5) where only the narrowband slope and complexity were differentially modulated by sleep stage and task demand.

Taken together, this suggests that the narrowband spectral slope and neural complexity actually track different features of brain activity that are only explicitly captured when using a restricted frequency range as for instance 30 – 45Hz. In broader frequency ranges, the dominance of other, especially lower frequencies might blur these effects, thus making them indistinguishable.

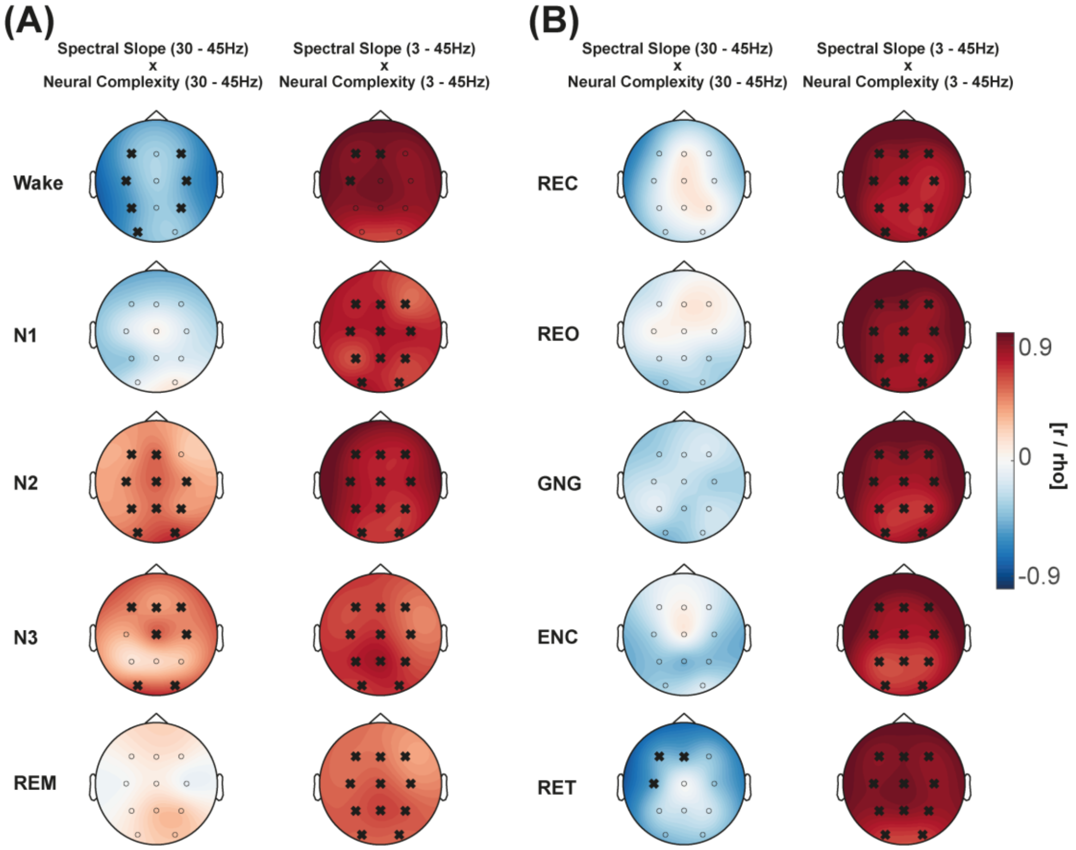

Figure 6. Summary of correlations between the spectral slope and neural complexity from 30 – 45Hz and 3 – 45Hz. The sleep (A) and task (B) data per subject were averaged across all lab-sessions. For task data, only the evening assessments highlighted by the dashed dark-green rectangle in Figure 1 were considered. Significant correlations ($p \leq .050$ after correcting for false discovery rate) are highlighted with a cross on the topographical maps (color codes for the size and directionality of the correlation coefficients). The 30 – 45Hz slope and neural complexity showed no consistent positive or negative relationship across tasks and sleep stages. In contrast, the 3 – 45Hz slope and neural complexity were consistently positively correlated over all tasks and sleep stages ($N = 28$).

Figure 6: Supplement 1. Correlation of the slope and complexity with themselves in the narrow- or broadband frequency range during sleep (A) and wakefulness (B). Only the spectral slope was consistently positively correlated with itself, whereas the complexity was slightly negatively correlated with itself between the two frequency ranges.

Lastly, we assessed how strongly the spectral slope and neural complexity were correlated with themselves in the different frequency ranges. The narrow- and broadband slopes were always positively correlated, whereas the opposite was true for neural complexity (see Figure 6 – Figure Supplement 1). Thus, flatter narrowband slopes were usually associated with flatter slopes in the broadband range, but lower narrowband complexity was often even associated with higher broadband complexity. This suggests that especially the narrowband spectral slope might measure a facet of the underlying brain activity that is not represented in the narrowband neural complexity.

The spectral slope as an electrophysiological marker of task performance

Having established that spectral slope and neural complexity are not only modulated by sleep but also differ between tasks in a frequency range specific manner, we next investigated their relationship with task performance. Thus, we correlated the spectral slope and neural complexity from the narrow- and broadband frequency ranges during the Go/Nogo task with the according performance scores (percentage of correct trials divided by median reaction time) over multiple sessions. Again, this allowed us to test the robustness of any correlations with behavior. Only flatter slopes in the narrowband range (30 – 45Hz) were consistently related to better task performance (see Figure 7). Neural complexity, on the other hand, did not correlate with performance, neither in the narrow- nor in the broadband (3 – 45Hz) range (see Figure 7 and Figure 7 – Figure Supplement 1). In the broadband range, the relationship with task performance was still consistently positive for both parameters but did not reach statistical significance. The fact that this positive relationship was strengthened and actually turned significant only for the slope in the narrowband range again suggests a distinct role of the narrowband slope, which might also be interpreted as a specific marker of task performance.

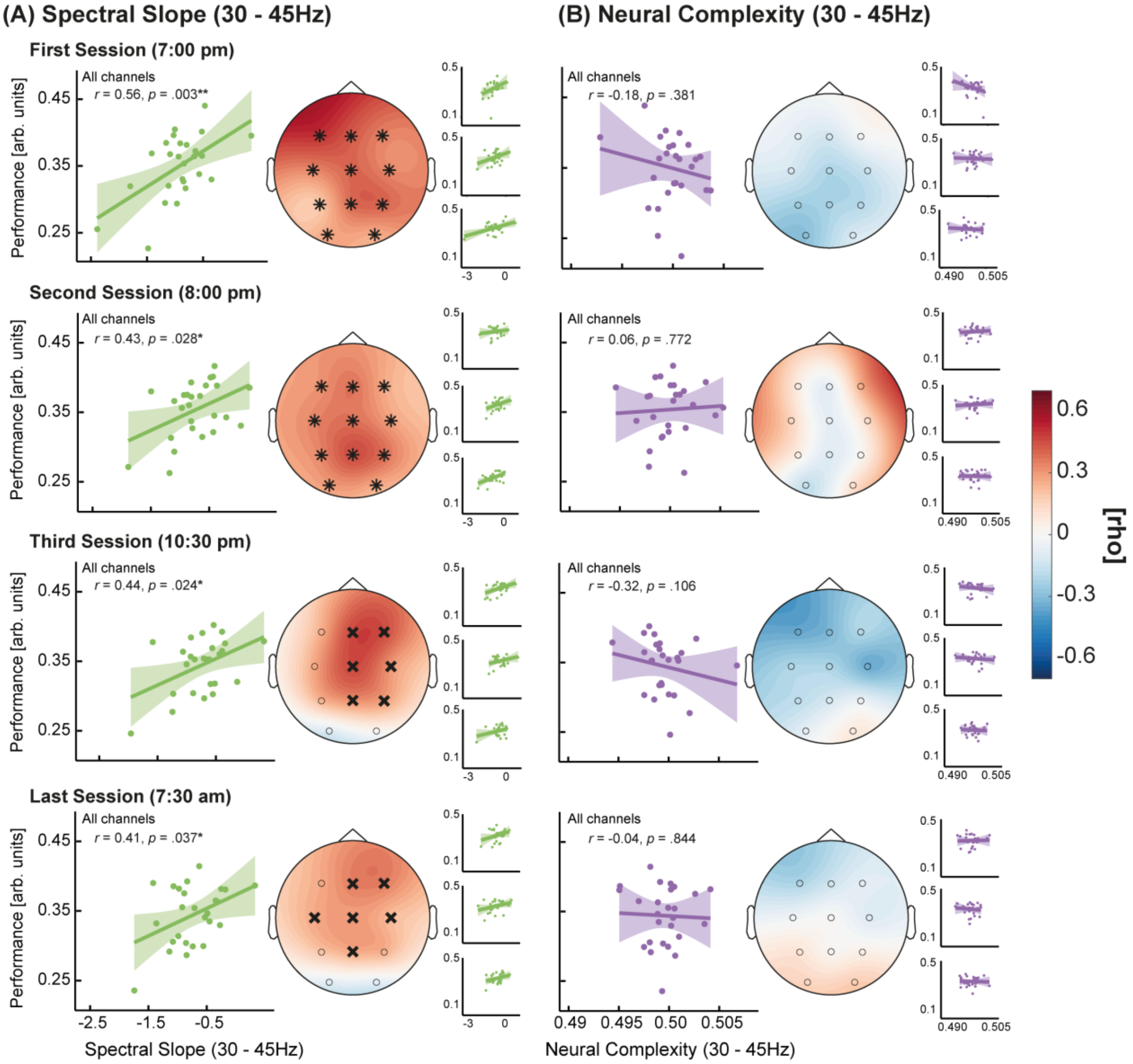

Figure 7. Relationship between Go/Nogo task performance and spectral slope (A) or neural complexity (B) within 30 – 45Hz across different assessment times. For the large scatterplots, the data was averaged across all lab-sessions (small scatterplots show the relationship in each lab-session). The topoplots depict the strength of the correlation for each electrode. Electrodes forming a significant cluster are highlighted with asterisks. Those showing a significant correlation after false discovery rate correction but did not from a significant cluster are marked with a cross. Only the narrowband spectral slope showed a consistent positive relationship with task performance (*N* = 26).

Figure 7: Supplement 1. Results when using the broadband (3 – 45Hz) frequency range. No significant relationships emerged for the spectral slope and neural complexity, even though the correlation was consistently positive for both parameters.

Next, we determined whether the narrowband spectral slope can even be used to track memory performance. Therefore, we correlated the spectral slope and neural complexity during the retrieval sessions of a declarative memory task with the recall performance scores (i.e., percentage of correctly recalled word pairs). Even though the overall pattern was similar to the Go/Nogo task, most correlation coefficients only showed a trend towards statistical significance (see Figure 8). Despite the lack of statistical significance on most electrodes, the narrowband spectral slope was again consistently positively correlated with recall performance. This indicates that flatter slopes, especially in the narrowband frequency range, are not only related to better attentional performance but might also benefit declarative memory. In contrast, the narrowband complexity was not positively correlated with memory performance and even expressed a negative relationship on some electrodes. Since we observed a positive relationship between overnight decreases in resting state slopes and memory performance in another study (Lendner et al., 2022), we further assessed whether the overnight change in slope during the retrieval task is also correlated with sleep-dependent memory consolidation. However, we did not obtain a significant relationship, indicating that while flatter slopes during the retrieval were associated with slightly better memory performance in the according session, overnight changes in the slope or complexity were not related to performance changes in our study.

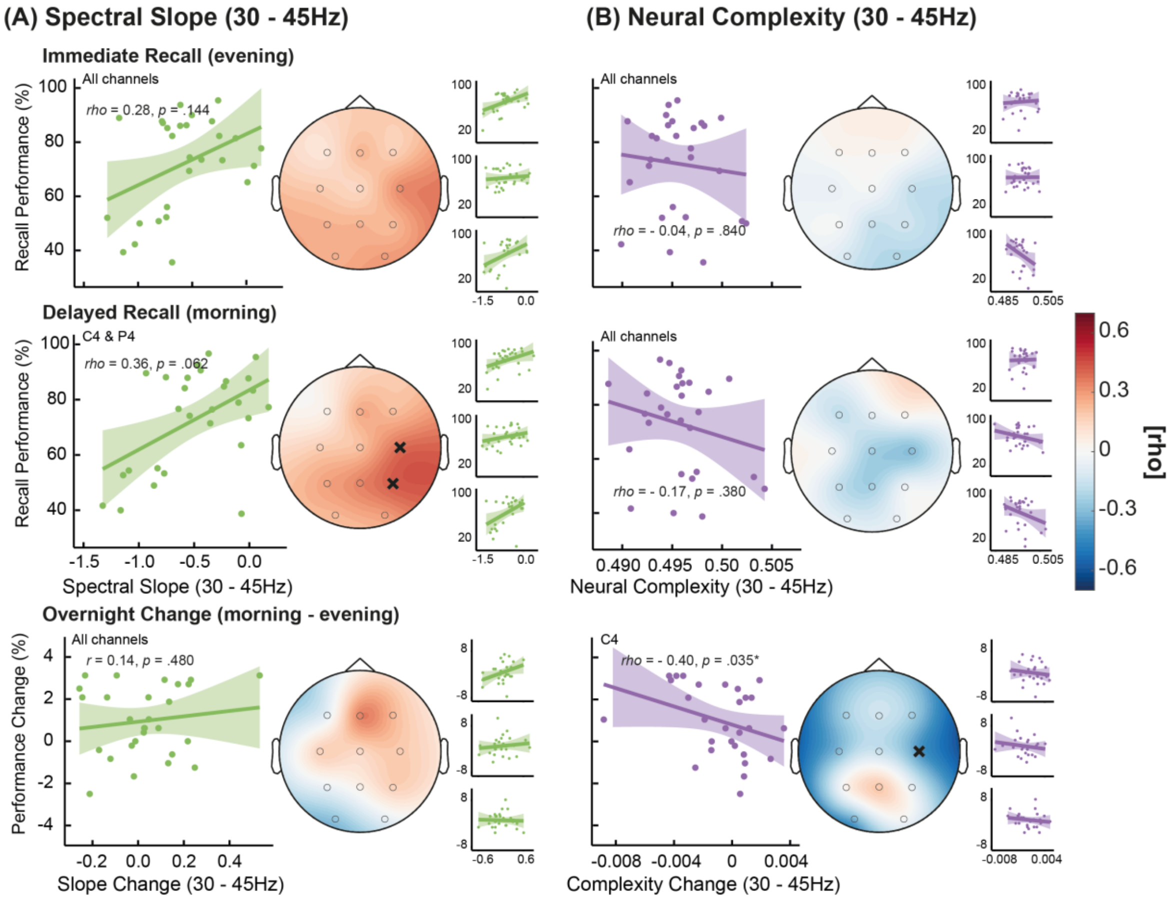

Figure 8. Relationship of declarative memory recall performance and spectral slope (A) or neural complexity (B) within 30 – 45Hz. Results are shown for the immediate recall during the evening and the delayed recall in the next

morning as well as for the overnight change. For the large scatterplots, the data was averaged across all lab-sessions (small scatterplots show the relationship for each session). The topoplots represent the strength of the correlations on each electrode and color codes for the size and directionality of the correlation coefficients. Even though the spectral slope was consistently positively correlated with recall performance, no electrodes formed a significant cluster. Significant single electrodes that survived false discovery rate correction are highlighted with a cross (*N* = 28).

Figure 8: Supplement 1. Results when using the broadband 3 – 45Hz frequency range. No relationship observable between recall performance and the slope or complexity.

In the broadband frequency range, both parameters did not show a consistent relationship with recall performance (see Figure 8 – Figure Supplement 1). Finally, we analyzed whether the similar results between the Go/Nogo and declarative memory task performance could be traced back to better overall attention and higher task engagement but there was no significant relationship between the performance scores from the two tasks (evening: *rho* = 0.10, *p* = .611; morning: *rho* = 0.06, *p* = .766). Thus, subjects that performed well in the Go/Nogo task did not necessarily achieve a high recall performance score in the declarative memory task.

Discussion

In this study comprising three experimental recordings with multiple measurements per subject, we demonstrated that the spectral slope and neural complexity both reliably delineate sleep stages and are modulated by task demand during wakefulness. Critically, we provided evidence that the correlation between spectral slope and neural complexity strongly depends on the frequency content, which alters their modulation across task demands and sleep stages. The narrowband (30 – 45Hz) spectral slope was best suited to differentiate REM sleep from wakefulness, even though the broadband (3 – 45Hz) slope and neural complexity were more strongly modulated by sleep stages in general. During wakefulness, increasing task demands are associated with flatter slopes in the narrow- and broadband range, but only with higher complexity in the broadband range. Critically, solely the narrowband spectral slope tracked task performance in an auditory attention task (Go/Nogo) as well as in a declarative memory task.

Sleep stage specific alterations of spectral slope and neural complexity

Our findings corroborate previous research which demonstrated that the spectral slope and neural complexity are sensitive markers of sleep depth (Abásolo et al., 2015; Bódizs et al., 2021; Lendner et al., 2020; Pascovich et al., 2022; Schartner et al., 2017; Tagliazucchi et al., 2013). Building upon these findings, we leveraged repeated EEG recordings per subject and confirmed that the two parameters can robustly differentiate all sleep stages from wakefulness. Overall, sleep stages could be better delineated when a broadband frequency range (3 – 45Hz) was used for calculation of the spectral slope and neural complexity. This is probably due to the fact that the broadband range encompasses the frequencies typically used for traditional sleep scoring, such as slow wave activity (0.5 – 4Hz) and sleep spindles (11 – 15Hz; Dijk, 1995), thereby increasing the sleep stage specific information in the underlying signal. However, only the spectral slope within the narrowband frequency range (30 – 45Hz) clearly distinguished REM sleep from all other sleep stages, which is in line with recent findings by

Lendner et al. (2020). This behavior of the narrowband spectral slope contradicted the overall modulation of slope and complexity in the broadband range, where both parameters showed a relative, more wake-like, increase during REM sleep. Since REM sleep (sometimes called 'paradoxical sleep'; Peigneux et al., 2001 or Siegel, 2011) is characterized by wake-like, but non-oscillatory brain activity (Blumberg et al., 2020; Peever & Fuller, 2017), these disparate results between the two frequency ranges suggest that the narrowband slope mainly measures non-oscillatory, aperiodic brain activity. The relative increase in broadband complexity during REM sleep has been attributed to higher levels of conscious content that accompany vivid dreaming and thus require more complex brain activity than deeper, mostly dreamless sleep stages (Lau et al., 2022; Mateos et al., 2018).

Recent modeling work has also linked especially the narrowband spectral slope with the excitation to inhibition (E/I) balance in the brain (Gao et al., 2017). Within this framework, steeper slopes during REM sleep potentially reflect stronger inhibitory brain activity. This might allow the brain to decouple from its environment and, by maintaining muscle atonia, to enable the consolidation of emotional memories and the experience of vivid dreams (Aime et al., 2022) without the danger of acting them out. The narrowband (30 – 45Hz) complexity, however, expressed a diverging pattern compared to the narrowband slope and stayed almost constant across all sleep stages with even a slight increase from N1 to N2 sleep. Even though our study is the first to directly compare spectral slope and neural complexity during sleep, the congruency of both measures within the broadband frequency range might not be surprising, since previous studies investigating the parameters individually have shown their decrease across sleep (Aamodt et al., 2021; Lendner et al., 2020; Miskovic et al., 2019; Pereda et al., 1998; Schartner et al., 2017). Although we were able to classify sleep stages consistently above chance level with both parameters, it should be noted that our classifier was trained and tested only on our data. Furthermore, we did not compare the performance of the spectral slope and neural complexity to other potentially powerful biomarkers. Therefore, it would be interesting to see how accurate sleep stages can be scored exclusively by means of the slope or complexity and how the two markers perform in comparison to other indices of sleep depth like heart rate variability and blood pressure (Kuula & Pesonen, 2021; Mitsukura et al., 2020; Radha et al., 2019; van de Borne et al., 1994) or accelerometric data from actigraphy (Lüdtke et al., 2021; Sadeh et al., 1989) and multisensor consumer-wearables (Ameen et al., 2019; Boe et al., 2019; Roberts et al., 2020; Tal et al., 2017).

Spectral slope and neural complexity are modulated by task demands

In addition to our findings during sleep, we demonstrate that the spectral slope and neural complexity track different levels of task demands. That the slope and complexity are in general also modulated during wakefulness is in line with other research (Jacob et al., 2021; Mediano et al., 2021; Sheehan et al., 2018; Waschke et al., 2021), however, to our best knowledge this is the first study assessing the effect of task demand and the influence of different frequency ranges on the two parameters. Similar to sleep, we observed a homogenous modulation of the broadband (3 – 45Hz) slope and complexity, where flatter slopes and higher complexity were associated with an increase in task demands. This pattern was identical for the narrowband slope but was inverted for the narrowband complexity, where higher task demands were accompanied by decreasing levels of complexity. In the E/I balance framework, flatter narrowband slopes are the result of higher excitation in the brain (Chini et al., 2022; Gao et al., 2017). Thus, our observed pattern of a flattening of the spectral slope with increasing task demands seems plausible as more difficult tasks require more cognitive resources and therefore lead to stronger excitatory brain activity (Harris & Thiele, 2011; He, 2011; Kanashiro et al., 2017). Unlike Waschke et al. (2021), who reported a stronger occipital flattening of the slope in a visual compared to an auditory task, we did not observe clear topographical differences between modalities, even though the attentional Go/Nogo task was entirely auditory except for a fixation-cross whereas the declarative memory task mainly relied on visual content. However, this lack of topographical distinctiveness might be due to a partial overlap between involved brain areas since both, auditory discrimination and learning involve frontotemporal brain regions (Ackerman, 1992; Halsband, 1998).

Differential contributions of narrow- and broadband frequency ranges

Based on the results from the broadband frequency range, it is tempting to assume that the spectral slope and neural complexity are indexing the same or at least very similar features of brain activity. Indeed, according to Medel et al. (2020), both parameters might actually be driven by the transition entropy of the underlying cortical system and flatter slopes as well as lower complexity values could be similarly characteristic of the same cortical states. However, the divergence between the narrow- and broadband slope and complexity during sleep and wakefulness clearly demonstrates that the two parameters cannot be used interchangeable. Instead, especially in a restricted frequency range, they track different facets of the underlying brain activity. Here, we revealed that this selected frequency range dramatically influences the information that the two parameters provide and therefore also their interrelation. Using a narrowband frequency range from 30 – 45Hz for estimation decreases the relationship between the spectral slope and neural complexity. During wakefulness, different contributions of oscillatory and aperiodic brain activity to the slope and complexity could account for their diverging patterns in the narrowband range. Although it appears paradoxical that flatter narrowband slopes, representing an increase in aperiodic activity, should be accompanied by a decrease in neural complexity, others have also reported this type of counterintuitive behavior of neural complexity. Mediano et al. (2021) showed that in MEG within 0.5 – 30Hz, active tasks actually exhibited lower complexity values compared to rested wakefulness. In addition, a recent review from Lau et al. (2022) discussed several studies that reported apparently contradicting modulations of neural complexity in different clinical conditions, where some report lower and others higher levels of complexity. Thus, the question whether higher neural complexity can always be clearly interpreted as more complex or irregular brain activity remains unclear. So far, the best explanation for the contradictory findings in the neural complexity literature is that higher complexity values can both represent either more complex or more random systems (La Torre-Luque et al., 2016), which makes it difficult to argue whether higher complexity always represents a healthier neurophysiological brain state. Interestingly, other studies also showed a strong relationship between different complexity or entropy measures and the spectral slope (Colombo et al., 2019; Miskovic et al., 2019; Waschke et al., 2017), thus, it would be interesting to investigate in the future what drives their shared information and under which circumstances (i.e., frequency ranges) this relationship vanishes.

The narrowband spectral slope as a unique marker of task performance

When relating the spectral slope and neural complexity to behavioral outcomes, we observed that only the narrowband slope within 30 – 45Hz was correlated with attentional task performance in an auditory Go/Nogo task across all recordings per subject. Thus, it appears that the narrowband slope serves as a particularly sensitive marker for task-dependent fluctuations in brain states associated with behavioral performance. This association between adaptively flatter slopes and better task performance might even translate to more general cognitive tasks that do not solely rely on attention since we also observed a consistent positive but weaker relationship with memory performance. In larger scale studies that rely on databases or in multicenter studies, which commonly have higher statistical power, however, the broadband slope and complexity were also significantly correlated with task performance. For instance, Mediano et al. (2021) and Waschke et al. (2021) found an association between task-specific attention levels and spectral slope or neural complexity in a broader frequency range. As in our study the correlation between the broadband slope and complexity with the Go/Nogo task performance was also consistently positive but too weak to reach statistical significance, these findings do not necessarily contradict our claim that the narrowband spectral slope is even more sensitive to adaptive task-dependent changes in brain state. In contrast, this shows that lower statistical power might suffice for the narrowband slope to index robust relationships with behavioral performance.

Limitations

It should be noted that the cognitive tasks were not specifically designed for the analyses of varying levels of task demand as the data presented here was obtained from a study that was originally designed for the investigation of short-wavelength light effects on sleep, attention and memory performance (cf., Höhn et al., 2021 and Schmid et al., 2021). In the future, it might be promising to contrast tasks that exclusively rely on different cognitive resources and sensory modalities (e.g., auditory vs. visual) to assess how spectral slope and neural complexity adapt topographically to different modalities. Even though we used only 11 scalp electrodes, we still robustly detected the effects of sleep stage and task demand, providing evidence for the power of the spectral slope and neural complexity as indices of different brain states. Nevertheless, research with high-density or intracranial EEG setups might further contribute to the understanding of which topographical areas are most influential in driving changes in slope or complexity across brain states. Finally, we only recruited healthy male adults in a restricted age range (18 – 25 years) in order to avoid potential sex differences and hormonal effects (Kozhemiako et al., 2021; Plamberger et al., 2021). Therefore, it is unclear to what extent our results generalize to other populations. While sex does not necessarily affect the spectral slope or neural complexity when controlling for overall signal amplitude (Bódizs et al., 2021; Tosun et al., 2019), age does seem to play an important role in terms of developmental changes in the spectral slope and decorrelation of brain activity, which begins during early childhood (Chini et al., 2022; Schaworonkow & Voytek, 2021) and lasts until late adulthood (Dave et al., 2018). While this task-independent flattening of the slope in older subjects has been associated with decline in cognitive functioning (Voytek et al., 2015), our results suggest that task-dependent increases in excitation (expressed by flatter slopes) might be beneficial for behavioral performance. Thus, an adaptive task-specific modulation of the slope in healthy individuals appears to be associated with better task performance and might index cognitive adaptability.

Conclusion

Taken together, our results demonstrate that the EEG spectral slope and neural complexity are powerful indices of different brain states during sleep and wakefulness. We provide robust evidence from multiple recordings of three within-subjects measurements, showing that sleep stages and task demands are reliably indexed by both, the spectral slope and neural complexity. Critically, we show that the selected frequency range has a strong impact on the interpretability and functional relevance of the two parameters. When trying to distinguish different brain states, the broadband spectral slope and neural complexity are more sensitive, however, only the narrowband spectral slope within 30 – 45Hz turned out to be a powerful index of behavioral performance and best suited to differentiate REM sleep from wakefulness and all other sleep stages.

Materials and methods

Key resources table

Reagent type (species) or resource	Designation	Source or reference	Identifiers	Additional information
Software, algorithm	Brain Vision Analyzer 2.2	Brain Products GmbH	RRID: SCR_002356	https://www.brainproducts.com
Software, algorithm	Adobe Illustrator CS6	Adobe Inc.	RRID: SCR_010279	
Software, algorithm	Fieldtrip (obob_ownft)	Oostenveld et al., 2011	RRID: SCR_004849	https://gitlab.com/obob/obob_ownft/
Software, algorithm	FOOOF (specparam)	Donoghue et al., 2020		https://fooof-tools.github.io/fooof/
Software, algorithm	ggplot-2	Wickham, 2016	RRID: SCR_014601	https://cran.r-project.org/web/packages/ggplot2/index.html
Software, algorithm	Lempel-Ziv complexity	Comsa, 2019		https://github.com/iulia-m-comsa/EEG/tree/master/Lempel-Ziv%20complexity
Software, algorithm	MANOVA.RM	Friedrich et al., 2019		https://cran.r-project.org/web/packages/MANOVA.RM/index.html
Software, algorithm	MATLAB 2018b	MathWorks Inc.	RRID: SCR_001622	
Software, algorithm	MVPA-light toolbox	Treder, 2020	RRID: SCR_022173	https://github.com/treder/MVPA-Light

Software, algorithm	Psychtoolbox PTB-3	Kleiner et al., 2007	RRID: SCR_002881	http://psychtoolbox.org/
Software, algorithm	RStudio 2021.09	RStudio Team	RRID: SCR_000432	
Software, algorithm	Somnolyzer 24 x 7	Koninklijke Philips N.V.		https://www.philips.co.in

Participants and inclusion criteria

We recorded data from 28 male participants (18 – 25 years; mean age 21.54 ± 1.90 years). Final sample sizes varied for each analysis between *N* = 26 – 28 as some participants had missing data for specific tasks or timepoints (the exact sample size for each analysis is provided in the corresponding figure captions). All participants were free of medication and did not suffer from a mental or physiological illness or from sleep problems. They adhered to a regular sleep-wake rhythm (i.e., regular bedtimes with about 8 hours of sleep per night) and refrained from drug abuse and above-average caffeine consumption (more than three cups of coffee per day) during participation. For screening purposes, all subjects filled in an entrance questionnaire in which we checked for sleep quality, mood, anxiety, perceived stress level and chronotype (see Supplementary file – Table 1). Written informed consent was obtained from every participant and all subjects were remunerated with either 100€ and 16 hours course credit or 50€ and 24 hours course credit. The study was approved by the local ethics committee of the University of Salzburg (EK-GZ: 16/2014) and conducted in agreement with the Declaration of Helsinki.

Experimental protocol

Study design

Each subject participated over a time span of 14 days, with an entrance examination marking day one (an outline of the study protocol is presented in Figure 1). From that day on, participants wore an actigraph (MotionWatch 8; CamNtech Ltd, Cambridge, England) and filled in daily online sleep protocols (LimeSurvey GmbH, Hamburg, Germany), which we used to check for compliance with a regular sleep-wake rhythm.

The first recording was scheduled on day four and was implemented only for adaptation purposes in order to avoid potential first night effects (Browman & Cartwright, 1980; Curcio et al., 2004). After placement of all EEG, ECG, EMG and EOG electrodes, the participants were familiarized with the resting and Go/Nogo tasks. Bedtime was scheduled for approximately 11:00 pm and the participants were woken up 8 hours after lights out before they left the laboratory at approximately 9:00 am.

The experimental recordings were scheduled on days 7, 10 and 13. Participants arrived at 6:00 pm and EEG, ECG, EMG and EOG electrodes were mounted. The recordings started with an initial resting session (3min eyes closed and 3min eyes open) and the Go/Nogo task (10min), which was followed by the encoding sessions (two times 14min) of a declarative memory task. Before the first cued recall, another resting and Go/Nogo session were conducted. Afterwards, the participants had a 1.5 hours break from the tasks, in which they read stories under different light conditions (for details cf., Schmid et al., 2021). Before going to bed at approximately 11:00 pm, participants completed the last resting and

Go/Nogo session of the day. After awakening, a morning session of resting and the Go/Nogo task as well as another recall from the declarative memory task were performed. During all wake-recordings, daylight mimicking room lights (provided by Emilum GmbH, Oberalm, Austria) were dimmed to 4.5 photopic lux and room temperature was adjusted via air conditioning based on participant's preferences.

Go/Nogo task

To assess objective levels of attention, we implemented an auditory version of the Go/Nogo paradigm (Donders, 1969) via the Psychophysics Toolbox (PTB-3; Kleiner et al., 2007) in MATLAB (Release 2018b, The MathWorks Inc., Natick, MA). Participants were asked to react as quickly as possible with a button press on a response time box (RTBox v5/6; Ohio State University, Columbus, OH) whenever they heard a 'Go' sound and needed to inhibit their reaction when a 'Nogo' sound was played. The task comprised 400 trials with Go sounds being presented in 80% of the trials and Nogo sounds occurring in the remaining 20% of trials (the order of Go and Nogo sounds was randomized each time). The two stimuli used for the Go and Nogo sounds were low- (1000Hz) and high-pitched (1500Hz) tones, which were presented for 50ms with a varying interstimulus interval (1480 – 1880ms). Whether the low- or high-pitched sound represented the Go-signal was determined by chance at the beginning of each session. Participants had to react within 500ms for the response to be considered valid, but responses were recorded until 1000ms post-stimulus with reaction times longer than 500ms being regarded as attentional lapses. From each session, the performance score was computed by dividing the percentage of correct trials by the median reaction time of all valid responses (≤ 500ms, no errors) in milliseconds (Figueiro et al., 2016; Höhn et al., 2021).

Declarative memory task

Participants encoded a set of 80 word pairs on days 7, 10 and 13. To avoid learning effects over time, a different but similarly difficult set of 80 word pairs was presented on each of the three days. The order of the sets was randomized across subjects. Each set was presented twice for 14min during encoding and the data from both encoding sessions was pooled for further analyses. Each word pair was presented for 1500ms and was followed by a fixation-cross for 8500ms. Participants were instructed to encode the word pair as vividly as possible during the presentation of the fixation-cross by imagining a semantic connection between the two words. During the cued recall sessions, only the first word of a pair was presented, and participants were asked to press a button on the response time box as soon as they remembered the second word. Whenever a button was pressed, the participant was instructed to name the missing word and a fixation-cross appeared for 3500ms while the experimenter noted the answer. When no button was pressed, the fixation-cross appeared automatically after 6500ms.

EEG recording and analyses

All electrophysiological data were recorded with a sampling rate of 500Hz via the BrainVision Recorder software (Version 2.11, Brain Products GmbH, 2015) using a 32 channel BrainAmp system (Brain Products GmbH, Munich, Germany). We placed 11 gold-cup electrodes (Grass Technologies, Astro-Med GmbH, Rodgau, Germany) according to the international 10-20 system on the positions: F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, O1 and O2. The average of positions A1 and A2 on the left and right mastoids was used for offline re-referencing as the data were online referenced against Cz. Fpz was used as ground electrode. Additionally, two EMG electrodes were placed on the musculus mentalis for measuring muscle activity during sleep and four EOG electrodes around the eyes to record horizontal and vertical eye movements. ECG was recorded with an electrode on the right clavicular and another one on the lowest left costal arch. Impedances were always kept below 10kΩ.

Polysomnography

The time in bed was standardized for all polysomnography recordings and comprised exactly 8 hours. For sleep staging, the data were first low-pass filtered at 30Hz and re-referenced to contralateral mastoids with the BrainVision Analyzer software (Version 2.2.0.7383, Brain Products GmbH, 2019). Physio-channels were referenced in a bipolar manner and the data were down-sampled to 128Hz before sleep stages were classified for each 30 second epoch with the Somnolyzer 24 x 7 algorithm (Koninklijke Philips N.V.; Eindhoven, The Netherlands) in accordance with the criteria of the American Academy of Sleep Medicine (Richard et al., 2012). The results were finally verified by a human expert scorer. The general sleep architecture of each night is presented descriptively in Supplementary file – Table 5.

EEG preprocessing

In a first step, the data were processed with the BrainVision Analyzer software, and we applied a 0.3Hz high-pass as well as a 50Hz notch filter. The EEG channels were re-referenced to linked mastoids and the online reference Cz was restored. We corrected for eye movements with the Gratton & Coles method (Gratton et al., 1983; only implemented for data during wakefulness) and ran an automatic artifact detection. The data were then down-sampled to 250Hz and exported for further analyses in MATLAB. The continuous data were de-trended and subsequently segmented into epochs of 4s for each task and sleep stage using the fieldtrip toolbox (Oostenveld et al., 2011). To be able to compare all task- and sleep-data, we decided to set the epoch-length to 4s as this enabled the best tradeoff between a sufficient number of epochs even for the shortest tasks (3min resting sessions) and an adequate frequency resolution within 0.5 – 45Hz. All artifact-containing epochs (defined as > 1% being detected as artifact) were removed for the following analyses. Since the remaining number of clean epochs from the different tasks (resting, Go/Nogo, encoding and retrieval) and sleep-stages (WAKE, N1, N2, N3 and REM) varied dramatically due to different recording lengths, we balanced the number of epochs across tasks and sleep-stages for the multivariate pattern analyses (MVPA) to ensure the validity of the classification results. In more detail, we set the maximum number of epochs for the MVPA analyses to the highest possible number of epochs from the shortest task (i.e., 45 epochs as the resting sessions only comprised 3min). To do so, we drew a random subset of 45 epochs from all data that contained more than 45 clean epochs. For all other analyses we used all available data to maximize the signal to noise ratio wherever possible (for the number of epochs used per task and sleep stage see Supplementary file – Table 6).

Spectral Slope

To obtain the spectral slope, we first calculated power-spectra between 0.5 – 45Hz from the preprocessed, 4s segmented data via the *mtmfft* method in Fieldtrip (Oostenveld et al., 2011) using a multi-taper approach (1Hz frequency smoothing; Lendner et al., 2020). To extract the spectral slope information, we applied robust linear fits (using the *robust fit* MATLAB function) in log-log space between 30 – 45Hz based on a previously established method (Lendner et al., 2020). We decided to use robust linear fits instead of using the *FOOOF* algorithm (alternatively known as *specparam*; Donoghue et al., 2020) for the narrowband frequency range since this approach has already been established to yield a sensitive aperiodic marker of arousal by Lendner et al. (2020) and because in this frequency range also the *FOOOF* would approximate a linear fit, thus leading to highly comparable results. However, for the broadband frequency range (3 – 45Hz), we applied the *FOOOF* algorithm to extract the slope as the linear fits would have been skewed by oscillatory bumps in the power spectrum.

Neural Complexity

We followed previous approaches (Mediano et al., 2021; Schartner et al., 2015) and calculated the Lempel-Ziv-Welch complexity (Lempel & Ziv, 1976; Welch, 1984) as a proxy for neural complexity per channel and epoch. To obtain the neural complexity in the same frequency ranges in which we calculated the spectral slope, we applied additional 3 or 30Hz high-pass and 45Hz low-pass filters to ensure that the underlying signal contained the same frequencies as for the spectral slope. As Rivolta et al. (2014) demonstrated that 1000 datapoints are sufficient for reliable Lempel-Ziv complexity analyses during sleep, we used the same 4s segmented data (which translates to 1000 sampling points per epoch in the down sampled data) for the neural complexity analyses that we used for the spectral slope. We then applied a Hilbert-transformation on each epoch to obtain the instantaneous amplitude. Afterwards, we binarized the resulting single epoch data around its median amplitude and transformed it into a binary sequence. Values of 1 were given for amplitude samples above the median and values of 0 for amplitudes below (or equal with) the median. This binary sequence of ones and zeros was finally subjected to the Lempel-Ziv-Welch complexity algorithm (Comsa, 2019) in MATLAB. To make sure that our results were not affected by different algorithm implementations, we additionally ran the original Lempel-Ziv algorithm (LZ76, implemented in MATLAB by Thai, 2012) but did not obtain any different results. Thus, only the results from the Comsa (2019) algorithm are reported.

Statistical analyses

Statistics were calculated in R-Studio (Version 4.1.2.; RStudio Team, 2021). MATLAB functions from the Fieldtrip toolbox and the ggplot-framework (Wickham, 2016) in R were adapted for data visualization.

Factorial analyses and correlations

All analyses involved three repeated measurements (on days 7, 10 and 13; cf., Figure 1) and therefore at least two factors (lab-session and task or sleep stage). Since in most cases at least one assumption for parametrical testing was violated, we decided to compute more conservative semi-parametrical analyses with the MANOVA.RM package (Friedrich et al., 2019). For these factorial analyses, data were averaged over all EEG electrodes to facilitate interpretation of the results. In the statistical results, we always refer to the Wald-Type-Statistics (WTS) with empirical p-values obtained from permutation resampling procedures and 10.000 iterations. Whenever multiple comparisons were conducted for follow-up testing, p-values were corrected for alpha error inflation with the Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995).

For correlation analyses, we computed Spearman rho coefficients instead of Pearson correlations whenever the normality assumption was significantly violated (indicated by Shapiro-Wilk tests) and in general for all cluster correlations on the whole scalp level. For the cluster corrected correlation approach, we used the Monte-Carlo method with 10.000 iterations to assess the relationship between the EEG parameters per channel and the behavioral measures.

Multivariate pattern analyses (MVPA)

Since it is difficult to take topographical patterns into account in classical factorial designs, we additionally computed multivariate pattern analyses using the MVPA-Light toolbox (Treder, 2020) in MATLAB to further exploit the information present in the complexity and slope data as patterns across electrodes. For each task and sleep stage, the complexity and slope from every epoch and electrode was fed into the classifier. Thus, the single epochs per subject were used for training and testing while the complexity and slope patterns over electrodes represented the multivariate information. For comparisons between more than two tasks or sleep stages, multiclass linear-discriminant analyses (LDA) were used and regular LDA for two-condition comparisons. We calculated classifier accuracies per subject via leave-one-out cross validation (LOO-CV) to account for the restricted amount of data available for training and testing in our sample. Since no effects regarding the different lab-sessions emerged, we pooled the data from the different lab-sessions for each subject in order to improve the reliability of the MVPA analyses.

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Competing interests

The authors do not declare any competing interests.

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Ethics

This study was conducted in accordance with the guidelines from the Declaration of Helsinki. Written approval was additionally provided by the local ethics committee of the University of Salzburg (EK-GZ: 16/2014).

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