Title: Time-Resolved Neural Oscillations Across Sleep Stages: Associations with Sleep Quality and Aging

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Abstract

Sleep is a fundamental physiological process critical to cognitive function, memory consolidation, emotional regulation, and overall health. This study investigates the relationship between EEG spectral power dynamics and key sleep metrics, including percentage of N3, biological age, percentage of REM, and total sleep time (TST). Using high-resolution spectral analysis, we examine how power across multiple frequency bands (0.1–50 Hz) evolves temporally across sleep stages and influences sleep architecture. Our results reveal an inverse relationship between high-frequency power (sigma, beta, and gamma) during the N1 and N2 stages and the subsequent percentage of N3, suggesting that excessive low-frequency power in N2 may disrupt the smooth progression into deep sleep. Additionally, we identify a negative correlation between low delta power (0.1–0.5 Hz) during N2 and both percentages of N3 and TST, challenging traditional views on the role of delta activity in sleep regulation. These findings advance the understanding of how brain activity across frequencies modulates sleep depth and duration, with implications for addressing age-related sleep declines.

Introduction

Sleep is a vital physiological process that is crucial in cognitive function, memory consolidation, brain immune system, emotional regulation, and overall health. The study of sleep architecture—how different stages of sleep unfold throughout the night—has advanced significantly, particularly with the use of electroencephalography (EEG) to measure brain activity. EEG provides a non-invasive method for capturing the electrical dynamics of the brain across sleep stages, such as wakefulness, rapid eye movement (REM) sleep, and non-REM (NREM) sleep. Understanding the spectral dynamics of EEG across sleep stages, particularly during NREM stage 3 (N3) and REM sleep, has been critical to unraveling how the brain restores itself during sleep and how this process changes with age.

EEG Sleep Dynamics

EEG measures the electrical activity of the brain by detecting the sum of excitatory and inhibitory postsynaptic potentials across large populations of neurons. Sleep stages are typically classified based on characteristic EEG patterns, including changes in frequency and amplitude of

oscillations. NREM sleep is divided into stages N1, N2, and N3, each representing progressively deeper sleep. N3, also known as slow-wave sleep during non-REM deep sleep (SWS), is characterized by the dominance of low-frequency, high-amplitude waves in the delta band (0.5–4 Hz) and is thought to play a key role in physical restoration, immune function, and memory consolidation (e.g., Tononi & Cirelli, 2006). REM sleep, on the other hand, is marked by fast, low-amplitude activity in the theta (4–7 Hz) and beta (13–30 Hz) ranges, similar to wakefulness, and is associated with dreaming, emotional processing, and memory integration (Nir & Tononi, 2010; Walker & Stickgold, 2004).

Spectral analysis of EEG signals, which decomposes the brain's electrical activity into its frequency components, has been widely used to study the dynamics of these sleep stages. Each sleep stage exhibits distinct spectral patterns, and shifts in spectral power across different frequencies can offer insights into the underlying neural mechanisms (Achermann and Borbély 1997). Delta activity, especially during N3, is often considered a marker of sleep pressure and homeostasis, with greater delta power reflecting higher sleep need (Borbély 1982). In contrast, REM sleep is associated with both low- and high-frequency activity, reflecting its unique role in integrating emotional and cognitive processes (Llinás and Ribary 1993).

Spectral components associated with awake and various sleep stages have been described in the literature. Specifically, as individuals fall asleep, high-frequency beta (13–30 Hz) and gamma (30–50 Hz) activity, associated with wakefulness and cognitive engagement, gradually decreases, giving way to lower-frequency rhythms. Early in sleep, alpha waves (8–12 Hz) diminish, and theta activity (4–7 Hz) becomes more prominent, particularly during the light sleep stages like N1 and N2 (Iber et al., 2007). Sleep spindles (12–15 Hz) and K-complexes, characteristic of N2, indicate the onset of deeper sleep and transitions toward N3, or slow-wave sleep (SWS), which is dominated by delta waves (0.5–4 Hz). This stage is crucial for physical restoration and memory consolidation (Tononi & Cirelli, 2006). As the sleep cycle progresses, the EEG shows a return to higher frequencies in the form of theta, beta, and gamma activity during REM sleep, which is characterized by brain activity resembling wakefulness and is crucial for emotional regulation and memory integration (Hobson & Pace-Schott, 2002; Nir & Tononi, 2010). Understanding

these spectral dynamics is vital for recognizing how brain states shift across sleep stages and how disruptions can affect sleep quality.

N3 and Slow-Wave Sleep

N3 is the deepest stage of NREM sleep and is dominated by high-amplitude waves in the delta range (0.5–4 Hz). It is considered the most restorative stage of sleep, contributing to physical recovery, memory consolidation, and synaptic homeostasis (Tononi & Cirelli, 2006). The homeostatic regulation of N3 sleep is governed by sleep pressure, which builds up during wakefulness and is reflected by increased delta power during N3 (Borbély, 1982). Slow-wave activity (SWA) during N3 is thought to coincide with the clearing of metabolic waste products from the brain, a process that is crucial for preventing neurodegenerative conditions (Xie et al., 2013). Furthermore, N3 is involved in memory consolidation, particularly in transferring information from short-term storage in the hippocampus to long-term storage in the neocortex (Diekelmann and Born 2010).

However, not all aspects of N3 are fully understood, especially the relationship between different EEG frequencies and N3 percentage (N3%), or the proportion of the night spent in N3 sleep. Research has largely focused on delta activity as a hallmark of N3, but less is known about the role of other frequency bands, such as sigma (12–15 Hz) and beta, in regulating or disrupting slow-wave sleep. Additionally, while increased delta power is generally considered beneficial, some studies have suggested that excessive slow-wave activity may interfere with the smooth progression of sleep architecture (Willi et al. 1998). These open questions highlight the need for more detailed investigations into how spectral power across multiple frequencies correlates with N3%, and how these dynamics might vary across individuals.

REM Sleep

REM sleep is distinct from NREM sleep in both its spectral characteristics and its functional role. It is marked by mixed-frequency EEG activity, including theta, alpha (8–12 Hz), beta, and gamma (30–50 Hz) bands, which are associated with cognitive and emotional processing during

dreaming (Nir and Tononi 2010)(Walker, 2009). REM sleep has been implicated in the consolidation of emotional memories and the regulation of mood (Van der Helm et al., 2011). Moreover, REM sleep plays a role in creativity and problem-solving by integrating disparate pieces of information across neural networks (Walker & Stickgold, 2004).

The percentage of REM sleep (REM%) relative to total sleep time is an important measure of sleep quality. Decreased REM% has been linked to mood disorders such as depression and anxiety (Cartwright et al., 1998), while increased REM% is often associated with better emotional regulation and cognitive performance (Cai et al., 2009). REM is also frequently disrupted in Parkinson's disease patients due to neurodegeneration in brainstem areas regulating sleep, often leading to REM sleep behavior disorder (RBD) and reduced muscle atonia during REM (Arnulf, 2012; Boeve et al., 2007). However, the precise relationship between EEG spectral power and REM% remains poorly understood, particularly how different frequency bands within NREM and REM stages influence REM%. Studies have yet to elucidate the dynamic interplay between NREM spectral power and subsequent REM sleep.

Sleep Duration and Spectral Power

Total sleep time (TST) and sleep continuity are essential components of sleep quality, with shorter or more fragmented sleep linked to adverse health outcomes, including impaired cognitive function, mood disorders, and metabolic dysfunction (Buysse et al., 2005; Van Cauter et al., 2008). EEG spectral power has been found to correlate with sleep duration in specific ways, such as increased delta activity being associated with longer sleep (Borbély 1982). However, excessive high-frequency activity, particularly in the beta and gamma ranges, can disrupt sleep continuity and lead to shorter TST (Li et al. 2019). Interestingly, pre-sleep EEG activity, particularly in the delta band, may predict total sleep duration, as greater cortical downregulation prior to sleep is associated with more efficient sleep onset and longer durations (Borbély et al. 1981).

The relationship between spectral power dynamics and sleep duration is likely mediated by individual differences in sleep architecture and homeostatic processes. For instance, high delta

power during the awake period has been linked to longer sleep durations (Achermann and Borbély 1997), while beta and gamma activity during sleep is often associated with reduced sleep efficiency (D. J. Dijk et al. 1991). Further research is needed to clarify how these spectral dynamics evolve across the night and how they predict overall sleep duration and quality.

Age-Related Changes in Sleep Architecture

Aging is associated with significant changes in sleep architecture, including reductions in total sleep time, slow-wave activity, and REM sleep (Mander, Winer, and Walker 2017); (Ohayon et al. 2004). Older adults tend to experience more fragmented sleep, with increased awakenings and reduced time spent in N3 and REM stages. These age-related changes in sleep are paralleled by alterations in EEG spectral power, particularly a marked decline in delta power during N3 sleep (Carrier et al. 2001). Studies have shown that slow-wave sleep decreases by up to 50% between young adulthood and middle age, with further reductions in older adults (Ohayon et al. 2004). This reduction in slow-wave activity has been linked to cognitive decline and the development of neurodegenerative conditions, such as Alzheimer's disease (Mander, Winer, and Walker 2017).

Moreover, aging is associated with an increase in high-frequency activity, particularly in the alpha and beta bands, during sleep. This shift towards higher-frequency activity has been linked to sleep fragmentation and poorer sleep quality in older individuals (Feinberg and Campbell 2010). The decline in slow-wave activity and increase in high-frequency power raise important questions about how spectral dynamics relate to sleep quality across the lifespan and how interventions could be tailored to mitigate age-related declines in sleep.

The Current Study

Despite the extensive research on EEG spectral power and sleep, several key questions remain unanswered. First, while delta activity has been widely studied, the role of other frequency bands, such as sigma and beta, in regulating N3 and REM sleep remains unclear. Additionally, it is not well understood how changes in spectral power over time influence sleep stage transitions and overall sleep architecture. The dynamic interplay between the pre-sleep brain state, spectral

power in different stages, and key sleep metrics such as N3%, REM%, and sleep duration is underexplored.

This study aims to address these gaps by analyzing the spectral power dynamics across different sleep stages and their relationship with N3%, REM%, and total sleep time. By examining how spectral power evolves temporally from one stage to another and how spectral dynamics correlate with these key sleep metrics, this analysis seeks to provide novel insights into how brain activity during sleep is organized and how it influences sleep quality. Furthermore, this study will explore how these relationships change with age, shedding light on the neural mechanisms underlying age-related declines in sleep quality. These findings could inform future interventions aimed at improving sleep through targeted modulation of specific EEG frequency bands.

Methods

Participants and Data Collection

EEG and polysomnographic (PSG) data were obtained from the Stanford Technology Analytics and Genomics in Sleep (STAGES) study (Zhang et al., 2018), which included 1137 subjects (mean age 46.35 ± 14.05 years). EEG recordings were sampled at 200 Hz, 250 Hz, or 500 Hz, depending on the subject, and were subsequently down-sampled to 100 Hz to ensure uniformity in the analysis. PSG recordings included standard EEG channels (e.g., F3, F4, C3, C4, O1, O2) for the detection of sleep stages and other relevant physiological measurements.

Sleep Stage Transition Selection

To investigate sleep stage transitions, only subjects who demonstrated at least 5 minutes of contiguous data within a sleep stage followed by a transition to the next sleep stage with a minimum of 5 more minutes were included in the analysis. This ensured that each stage transition contained sufficient data for spectral analysis. Specifically, four transitions were analyzed:

- Awake to N1 (n = 425)
- N1 to N2 (n = 153)
- N2 to N3 (n = 492)
- N2 to REM (n = 538)

For each transition, data from the five minutes preceding and the five minutes following the transition were extracted for further analysis. This resulted in 10-minute segments (6000 time points) per subject and transition, which were then used for spectral analysis.

Time-Frequency Analysis

A fast Fourier transform (FFT) was applied to the EEG data to compute spectral power for each subject during the transition periods. The analysis was performed on consecutive, overlapping 10-second epochs (1000 samples) with a step size of 10 milliseconds, resulting in high temporal resolution. Spectral power was calculated in 0.1 Hz frequency steps from 0.1 Hz to 50 Hz. The spectral power values for each time step were normalized by dividing by the mean power across frequencies for each subject to account for individual and temporal variability in baseline power.

Time-frequency plots were generated by averaging the normalized spectral power across all subjects for each transition type. These plots represented changes in spectral power from -5 minutes to +5 minutes around the transition in 10 ms increments. The frequency resolution ranged from 0.1 Hz to 50 Hz, providing detailed insights into power changes across the entire transition period.

Linear Regression Analysis for Sleep Stage Transitions

To examine linear trends in spectral power during each transition, linear regressions were performed. For each subject, spectral power at each frequency (from 0.1 Hz to 50 Hz) was regressed against time during the 10-minute segments around each stage transition. This regression analysis was conducted independently for each transition type:

- **Awake to N1:** To study the changes associated with the onset of sleep.
- **N1 to N2:** To analyze the deepening of NREM sleep.
- **N2 to N3:** To capture transitions into slow-wave sleep (SWS).

- **N2 to REM:** To investigate transitions into REM sleep.

For each regression, the slope of the regression line and the standard error were calculated and then converted to a t-statistic, which indicated the direction and significance of the linear change in spectral power over time. The resulting t-values were averaged across all subjects for each frequency and transition type. The averaged t-values were then plotted alongside the time-frequency plots to show where significant increases or decreases in power occurred during each stage transition.

Overnight Regression Analysis of Spectral Power

A separate set of linear regression analyses was conducted to study the changes in spectral power over the entire course of a night's sleep. For each subject, spectral power at each frequency (0.1 Hz to 50 Hz) was regressed against time within each sleep stage (awake, N1, N2, N3, REM) across the entire night. The slopes and standard errors from these regressions were converted to a t-statistic and then averaged across subjects and plotted as a function of frequency for each stage, providing a comprehensive view of spectral changes throughout the night.

Correlation Analysis: Spectral Power and Sleep Metrics

To explore the relationship between spectral power and key sleep-related metrics, a series of Pearson correlation analyses were performed. Four metrics were considered:

1. Percentage of N3 sleep relative to total sleep time (N3%)
2. Percentage of REM sleep relative to total sleep time (REM%)
3. Total sleep time (TST)
4. Age of the subject

For each subject, the spectral power calculated for all 10-second epochs within each sleep stage (awake, N1, N2, N3, REM) was averaged to yield a mean power value for each frequency (0.1 Hz to 50 Hz) within each stage. These average spectral power values were then correlated with each of the four metrics across all subjects. The false discovery rate (FDR) correction was applied to account for multiple comparisons ($p = 0.125$ due to 4 sets of comparisons), and significant correlations were identified and reported.

Correlation Analysis by Sleep Stage

- **Awake:** Correlations between spectral power during the awake period and the four metrics (N3%, REM%, TST, and age) were calculated to assess how pre-sleep brain activity might influence sleep architecture and quality.
- **N1:** Correlations were computed to investigate how early-stage sleep (N1) activity relates to sleep outcomes and age.
- **N2 and N3:** N2 and N3 correlations were critical for understanding the relationship between deeper NREM sleep activity (e.g., delta waves) and metrics such as N3% and age.
- **REM:** The correlation between REM spectral power and each metric provided insight into how REM activity is linked to sleep health and age.

Correlation Analysis: Temporally Regressed T-Values and Sleep Metrics

In addition to correlating raw spectral power, a secondary analysis involved correlating the temporally regressed t-values from the linear regression analyses described above with the four sleep metrics (N3%, REM%, TST, and age). This allowed for the examination of how linear changes in spectral power over time during each stage and frequency band were associated with sleep quality and aging.

Correlation Analysis by Sleep Stage

- **Awake:** Temporal changes in spectral power during the awake period were correlated with sleep metrics, providing insight into how pre-sleep changes in brain activity might predict sleep quality (e.g., more REM or longer TST).
- **N1:** Temporal trends in N1 activity were examined for their association with sleep metrics, such as how gradual changes in early-stage sleep might correlate with increased N3% or TST.

- **N2 and N3:** The temporal evolution of spectral power in N2 and N3 stages was particularly relevant for understanding slow-wave activity changes over the course of the night and how these changes correlate with sleep metrics such as N3% and TST.
- **REM:** Temporal changes in REM spectral power were examined to assess whether gradual increases or decreases in activity over the night were associated with changes in REM%, TST, or age.

The FDR correction was applied to both the spectral power correlations and temporally regressed t-value correlations, , and statistically significant relationships were highlighted. These analyses provided insight into how both static and dynamic changes in spectral power during sleep correlate with overall sleep quality and age.

Results

Time-Frequency Analysis of Sleep Stage Transitions

Awake to N1 Transition

The transition from wakefulness to the initial stage of sleep, N1, revealed significant shifts in spectral power across several frequency bands (**Figure 1**). Specifically, there was a substantial decrease in high-frequency activity (beta and gamma bands, 16–50 Hz), aligning with prior findings of reduced cognitive and cortical arousal as individuals enter light sleep (Ray and Cole 1985); Cantero et al. 2004). Simultaneously, power increases were observed in lower frequencies, particularly in the delta (0.1–4 Hz) and theta (4–7 Hz) bands. These shifts in low-frequency power are consistent with early-stage sleep characteristics, which have been associated with early brainwave synchronization and the onset of sleep spindles (Steriade, McCormick, and Sejnowski 1993). Additionally, a modest increase in sigma band (13–15 Hz) power was observed, which may reflect the initiation of sleep spindle activity, a marker of NREM sleep onset (De Gennaro and Ferrara 2003).

N1 to N2 Transition

During the transition from N1 to N2 sleep (**Figure 2**), the most notable changes in spectral power occurred in the beta and gamma bands (16–50 Hz), where a pronounced decrease was observed. This is consistent with previous studies that have shown a progressive reduction in higher-frequency activity as sleep deepens (Germain et al. 2007). Power in the lower frequencies, particularly in the delta (0.1–4 Hz) and theta (4–8 Hz) bands, continued to increase, indicating further cortical synchronization. Notably, the increase in sigma band power during N2 is reflective of sleep spindle activity, which is crucial for memory consolidation (Fogel and Smith 2011). Our results corroborate earlier findings that suggest N2 is characterized by heightened spindle activity and continued reductions in faster frequencies as the brain transitions into deeper sleep (Fernandez & Lüthi, 2019).

N2 to N3 Transition

The transition from N2 to N3, or deep slow-wave sleep (SWS), exhibited relatively fewer significant changes in spectral power compared to earlier transitions (**Figure 3**). A broad and consistent decrease in alpha to beta and gamma (8–50 Hz) activity was observed, in line with previous studies reporting a reduction in sleep spindle activity and higher-frequency activity as the brain moves into SWS (Mölle et al. 2002). The most pronounced change was a modest increase in low delta activity (0.1–0.4 Hz), reflecting the characteristic slow waves of deep sleep (Achermann and Borbély 1997) with a peak at 0.7 Hz. These findings are consistent with studies reporting that slow-wave activity (SWA) dominates N3 sleep and is essential for restorative functions (Tononi and Cirelli 2006).

N2 to REM Transition

The N2 to REM transition demonstrated smaller but significant spectral shifts (**Figure 4**). High-frequency beta and gamma activity (16–50 Hz) increased, a pattern that aligns with REM's characteristic high cortical activation and fast, desynchronized EEG patterns (Llinás and Ribary 1993). In contrast, power in the delta (0.5–3 Hz) and sigma (12-15 Hz) bands showed a decrease during REM, suggesting a combination of high arousal and low-frequency desynchrony that characterizes this stage (Insana 2020) with a final reduction in SWA and sleep spindles before entering REM. These results are consistent with reports of mixed-frequency activity during

REM, which may contribute to its role in emotional processing and dreaming (Nir and Tononi 2010).

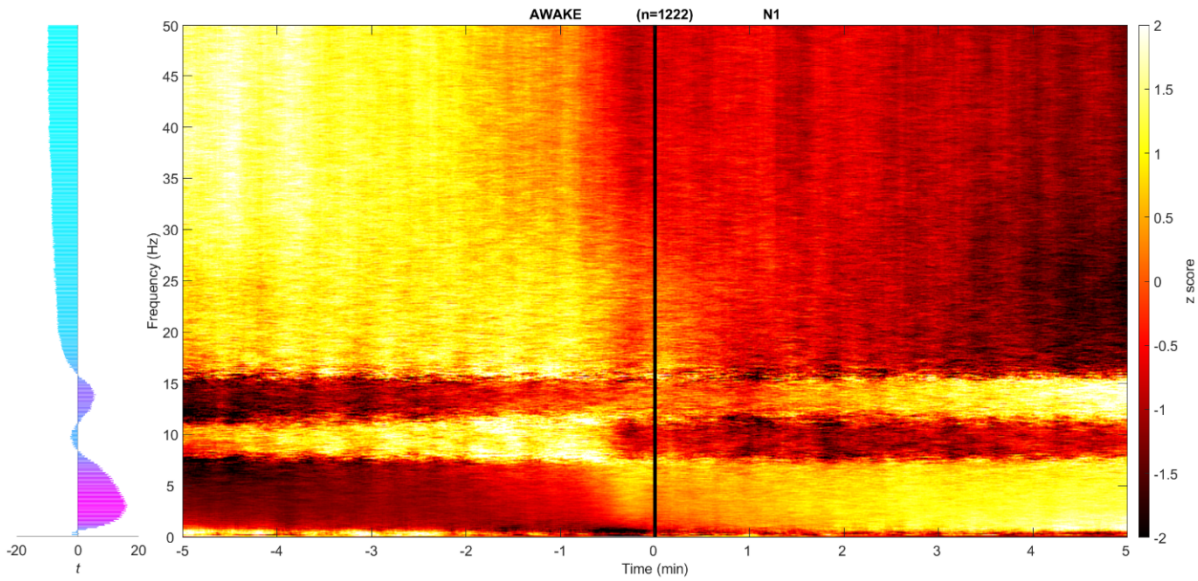

Figure 1. Spectral Power Changes During the Transition from Wakefulness to N1 Sleep

Figure 1. Time-frequency analysis of EEG spectral power changes during the transition from wakefulness to N1 sleep. The heatmap represents the averaged power spectra across all participants, with frequency on the y-axis (0.1 to 50 Hz) and time relative to the transition (in minutes) on the x-axis. Lighter colors, such as orange and yellow to white, indicate increased power, while darker colors, such as red and dark red to black, represent decreases. *t* values corresponding to temporal regressions over the 10 min time period are plotted to the left with increasing *t* values as power increases over time displayed as purple to magenta and decreasing *t* values as power decreases over time displayed as blue to cyan.

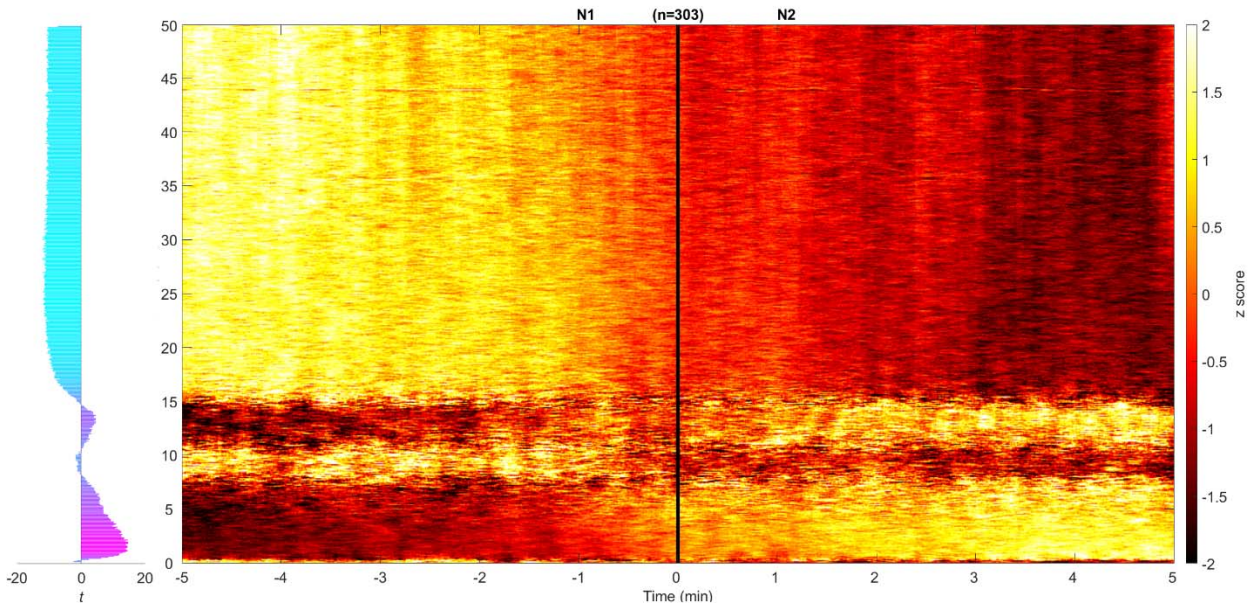

Figure 2. Spectral Power Changes During the Transition from N1 to N2 Sleep

Figure 2. Time-frequency analysis of EEG power changes during the transition from N1 to N2 sleep for a -5 to 5 min period with corresponding temporal regressions in power plotted on the left.

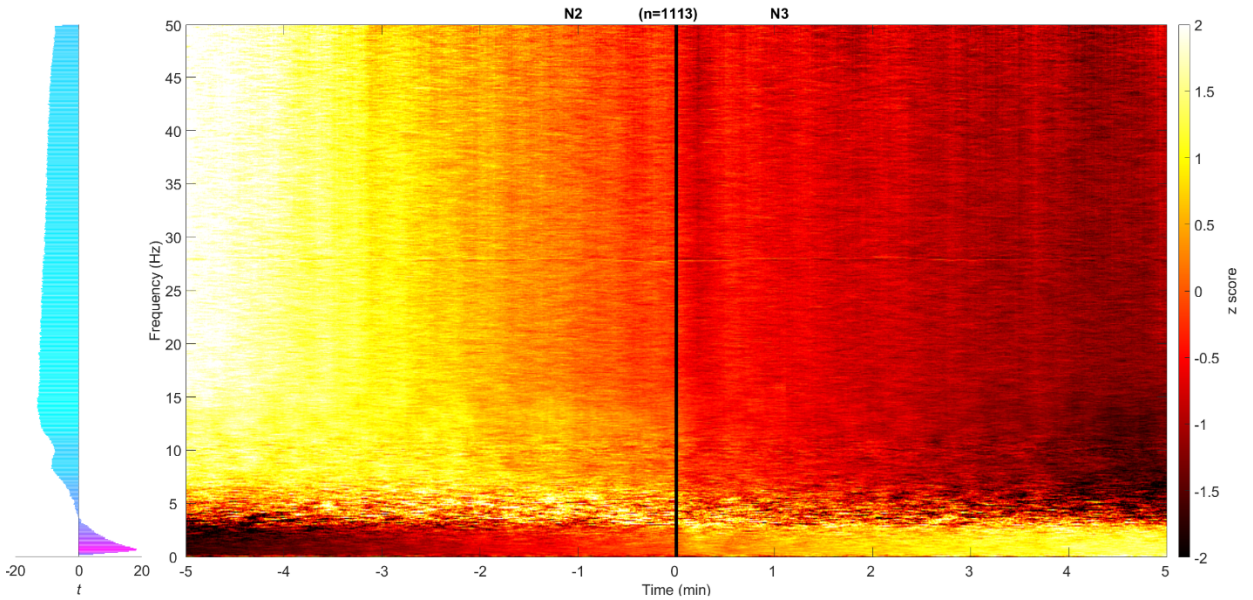

Figure 3. Spectral Power Changes During the Transition from N2 to N3 Sleep

Figure 3. Time-frequency analysis of EEG power during the transition from N2 to N3 sleep for a -5 to 5 min period with corresponding temporal regressions in power plotted on the left.

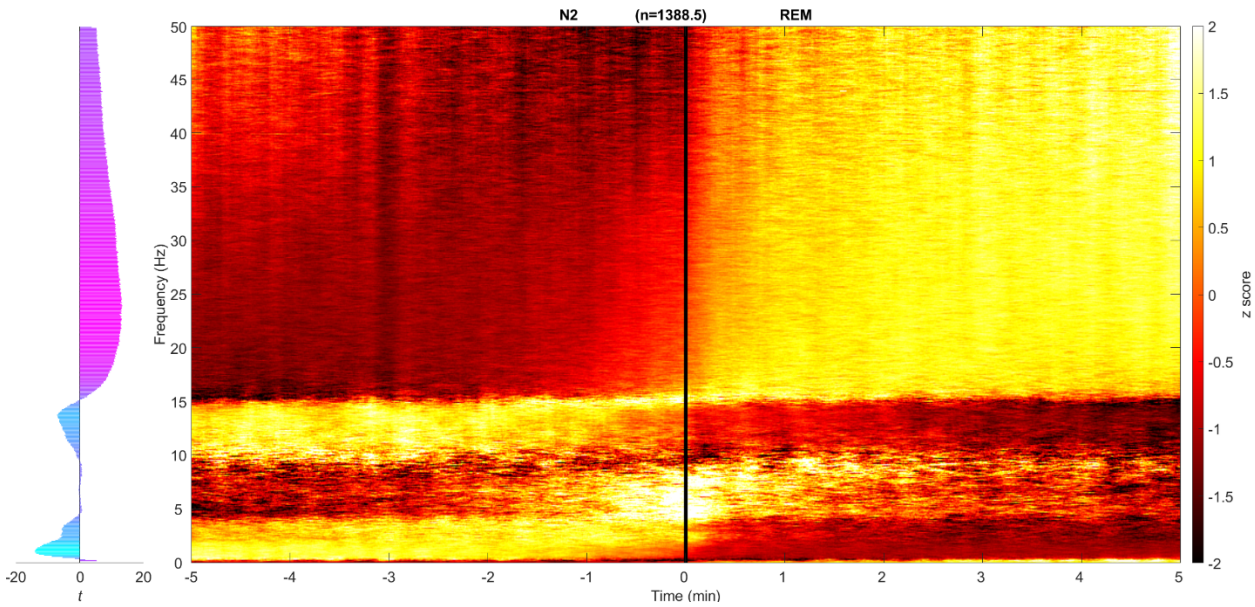

Figure 4. Spectral Power Changes During the Transition from N2 to REM Sleep

Figure 4. This figure illustrates the time-frequency analysis of EEG power changes during the transition from N2 to REM sleep for a -5 to 5 min period with corresponding temporal regressions in power plotted on the left.

Linear Regression Analysis for Sleep Stage Transitions

We conducted a temporal regression analysis to examine linear changes in spectral power across the entire night within each sleep stage (**Figure 5**). While fluctuations in power were observed across all five stages (awake, N1, N2, N3, and REM), only a few trends reached statistical significance. In N2, delta power (0.5–3 Hz) showed a significant decrease over time, suggesting a reduction in slow-wave activity as the night progressed. In contrast, during N3, the very low delta band (0.1–0.5 Hz) exhibited a significant increase in power over time, indicating a progressive deepening of slow-wave activity within this stage. These findings have not previously been reported in the literature and they highlight the dynamic nature of delta activity, with distinct temporal patterns across NREM stages.

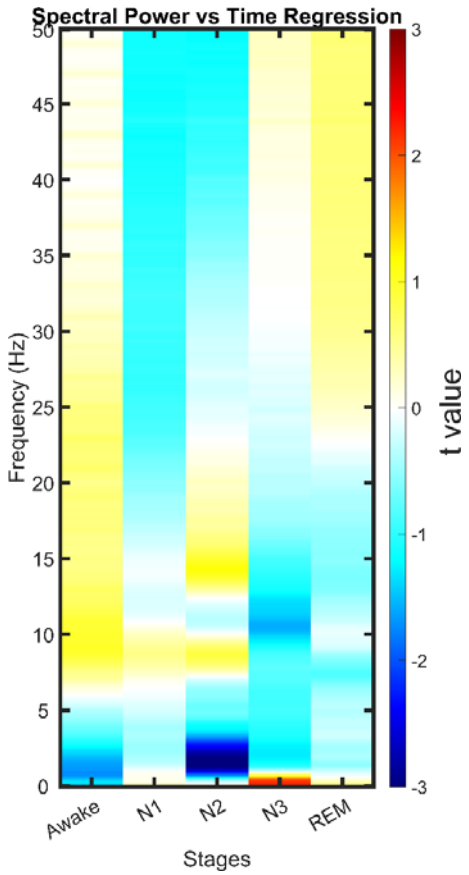

Figure 5. Temporal regression of spectral power across sleep stages and frequencies.

Figure 5. This figure shows the results of linear regression between time and spectral power across different sleep stages (awake, N1, N2, N3, and REM) and frequencies from 0.1 to 50 Hz. Warm colors (orange to red) represent positive regressions, indicating increases in spectral power over time, while cool colors (cyan to blue) represent negative regressions, indicating decreases. Statistically significant regions ($p < 0.05$, FDR-corrected) are colored.

Correlation Analysis of Spectral Power and Sleep Metrics

N3 Percentage

Across all sleep stages, N3% negatively correlated with spectral power in multiple frequency bands (**Figure 6**). Notably, there was a strong negative correlation between sigma power (11-15 Hz) during N1 and N3%, suggesting that more spindle activity in N1 is associated with less deep sleep later in the night (Mölle et al. 2002). A similar negative correlation was observed between very low delta (0.1–0.5 Hz) power during N2 and N3%, indicating that greater low-frequency

activity in early stages may limit subsequent slow-wave sleep (Dijk 2009). Additionally, less beta and gamma power during N2 and REM strongly correlated with more N3, a surprising finding for REM as typically higher-frequency power increases during that stage. These findings align with studies showing that increased N2 spindle activity can reduce the duration of deep sleep (Fogel SM et al. 2007).

REM Percentage

For REM%, a weak but significant negative correlation was found with spectral power in the alpha to gamma range across several stages (**Figure 6**). This suggests that lower cortical activation in all stages of sleep is associated with more REM sleep. Interestingly, a positive correlation was observed between delta activity during wakefulness and REM%, suggesting that higher pre-sleep delta power may promote REM sleep, possibly through a homeostatic mechanism (Borbély 1982).

Sleep Duration

Sleep duration correlated negatively with high-frequency activity (alpha to gamma, 7–50 Hz) across multiple stages (**Figure 7**), indicating that reduced cortical activation during sleep is also associated with longer total sleep time (TST). In contrast, a strong positive correlation was found between delta power during the awake period and TST, suggesting that higher levels of pre-sleep delta activity may predict longer sleep duration (Borbély et al. 1981). This result highlights the importance of pre-sleep cortical downregulation for overall sleep quality.

Age

As expected, age was positively correlated with beta and gamma power during the awake period (**Figure 7**), suggesting increased cortical activation in older adults prior to sleep (Carrier et al. 2001). During N1, N2, and REM, we observed a positive correlation between alpha-to-beta power and age, which is consistent with studies showing that older adults exhibit greater high-frequency activity and less slow-wave activity during sleep (Ohayon et al. 2004). Notably, negative correlations were found between delta power in N3 and sigma power in N2 and N3 and

age, confirming that slow-wave activity declines with aging (Mander, Winer, and Walker 2017), Mander et al., 2013).

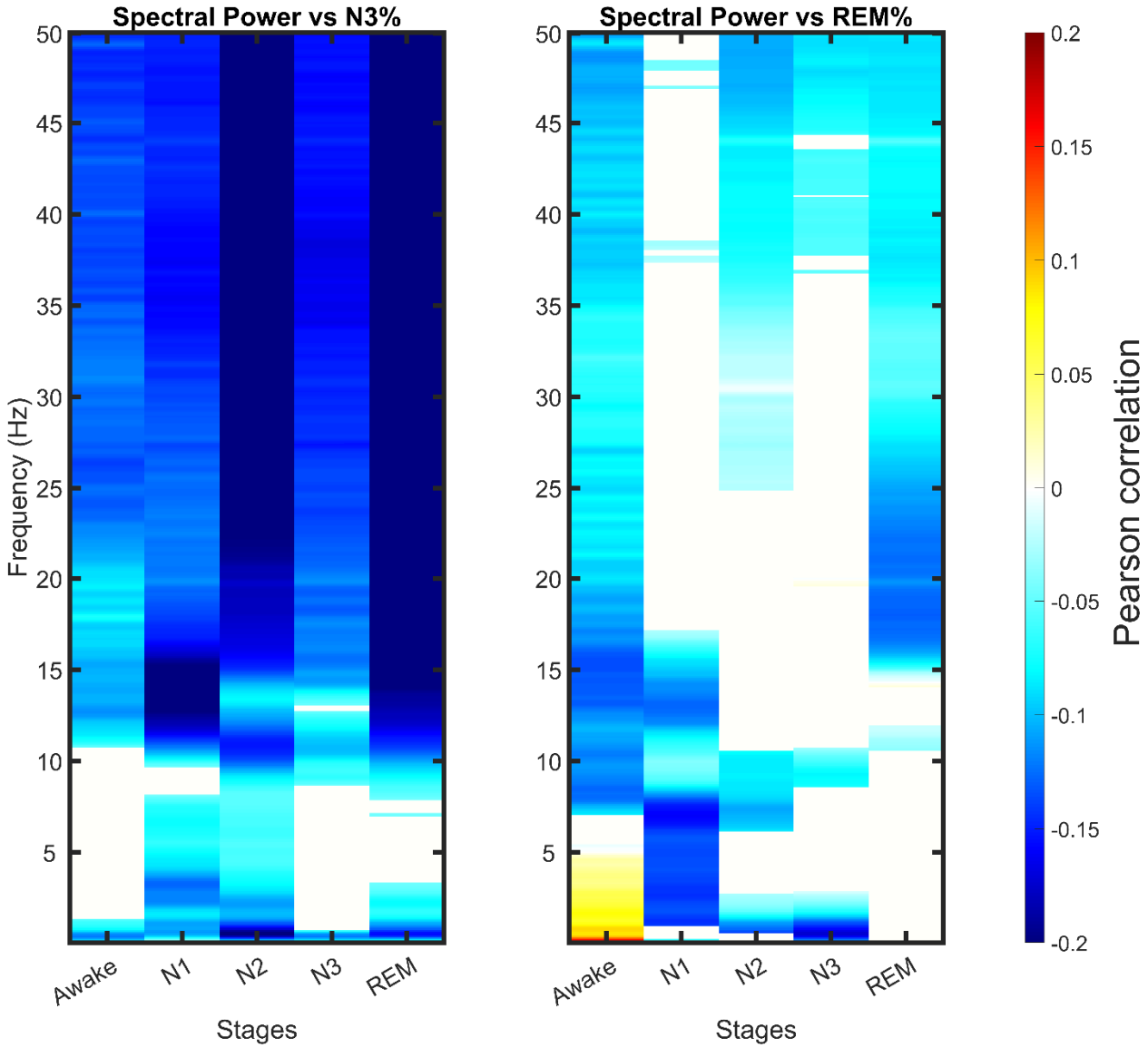

Figure 6. Correlations of spectral power with N3 percentage (left) and REM percentage (right) across sleep stages and frequencies.

Figure 6. This figure displays the correlation results between spectral power and the percentage of N3 sleep (left) and REM sleep (right) for each sleep stage (awake, N1, N2, N3, and REM) and frequency from 0.1 to 50 Hz. Warm colors (yellow to red) represent positive correlations, where higher spectral power is associated with greater N3 or REM percentage, while cool colors (cyan to blue represent negative correlations. Statistically significant regions ($p < 0.05$, FDR-corrected) are colored.

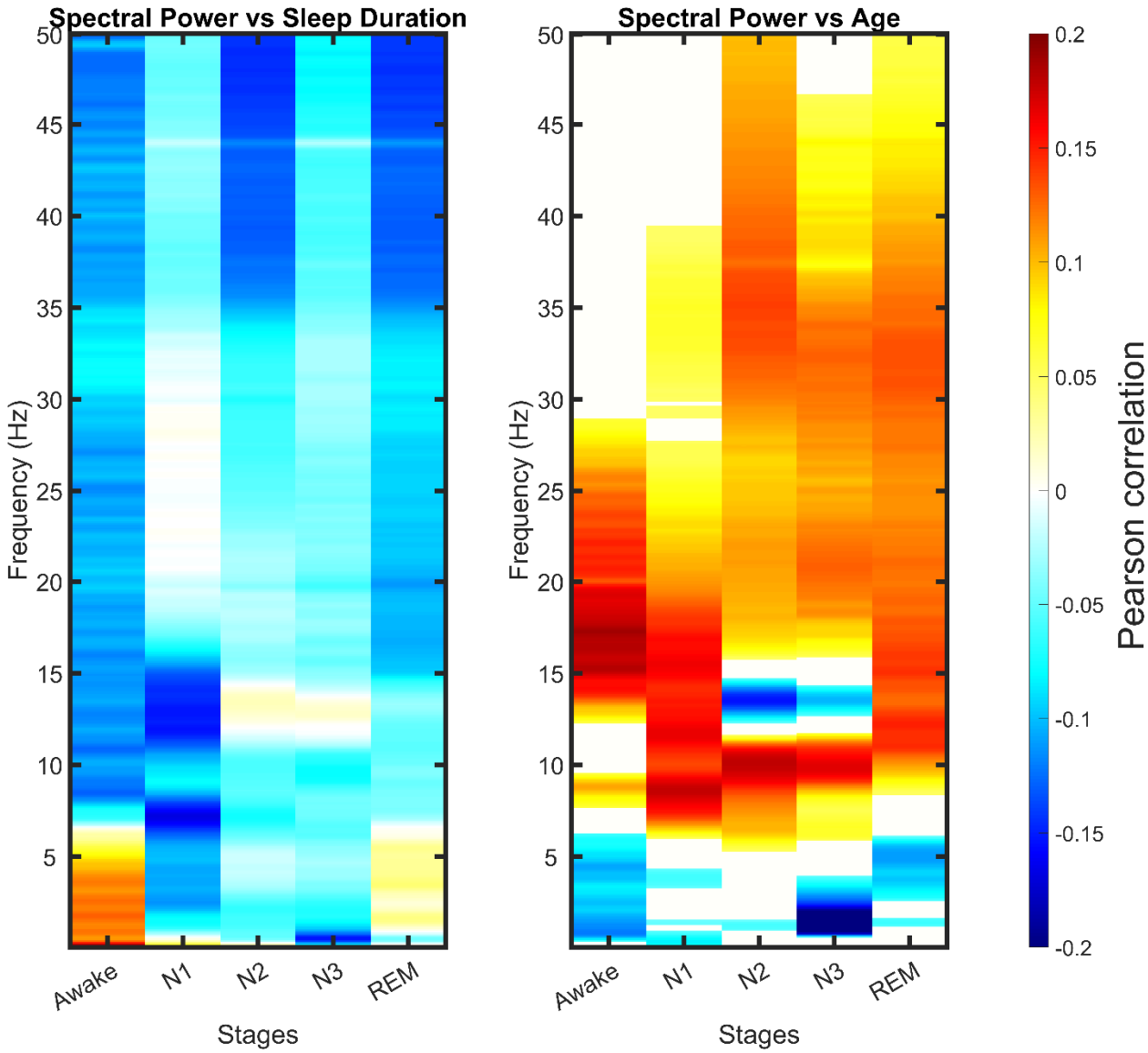

Figure 7. Correlations of spectral power with sleep duration (left) and age (right) across sleep stages and frequencies.

Figure 7. This figure presents the correlation results between spectral power and total sleep duration (left) and age (right) for each sleep stage (awake, N1, N2, N3, and REM) and frequency range from 0.1 to 50 Hz. Warm colors (yellow to red) indicate positive correlations, showing that higher spectral power is associated with longer sleep duration or greater age, while cool colors (cyan to blue) indicate negative correlations. Statistically significant regions ($p < 0.05$, FDR-corrected) are colored.

Correlation Analysis of Temporally Regressed T-Values and Sleep Metrics

N3 Percentage

The temporal regression analysis revealed that greater decreases in sigma and low beta (11–19 Hz) power over time during the awake period were associated with higher N3% across the night (**Figure 8**). This suggests that individuals who exhibit consistent increases in cortical downregulation during wakefulness may experience more slow-wave sleep, aligning with findings that efficient pre-sleep deactivation is crucial for deeper sleep (Massimini et al. 2005). During N2, increases in delta power over time were strongly correlated with higher N3%, further emphasizing the role of delta activity in promoting slow-wave sleep over time (Tononi and Cirelli 2006). The same was true during N3 but for a more narrow and lower delta band (0.1-0.7 Hz) and a negative relationship was observed for higher delta to theta (1-7 Hz) such that decreases in power over time during N3 led to more N3 throughout a night.

REM Percentage

For REM%, increased delta power over time during wakefulness was positively correlated with more REM sleep (**Figure 8**), suggesting that pre-sleep cortical downregulation may facilitate REM sleep. Additionally, decreases in delta power during N3 and REM were associated with lower REM%, indicating that sustained slow-wave activity in N3 may limit REM sleep, which is in line with findings that excessive slow-wave activity can inhibit REM (Bódizs et al., 2005). A narrow sigma band (13-15 Hz) of activity during N3 was shown to increase over a night of sleep, leading to more REM sleep.

Sleep Duration

Temporal regression analyses showed that increased delta power during wakefulness was positively correlated with total sleep time (TST). This finding (**Figure 9**) supports the hypothesis that higher levels of pre-sleep cortical downregulation are predictive of longer sleep durations (Borbély et al. 1981). Additionally, the same relationship was shown for alpha during N1, sigma to beta in N2, and beta to gamma in N3. In contrast, decreases in delta power during N2 and N3 were negatively correlated with TST, suggesting that decreasing slow-wave activity in these

stages may promote longer sleep duration, consistent with the restorative role of slow-wave sleep (Mander, Winer, and Walker 2017).

Age

Regarding age, temporal regressions indicated that older adults exhibit decreasing very low delta (0.2-0.7 Hz) power over time during N3 (**Figure 9**) while higher delta and theta power increased over time, reflecting part of the age-related decline in slow-wave activity (Ohayon et al. 2004). In contrast, a negative correlation was found between age and decreasing theta activity during REM. These results confirm previous findings on the reduction of slow-wave activity with age (Mander, Winer, and Walker 2017).

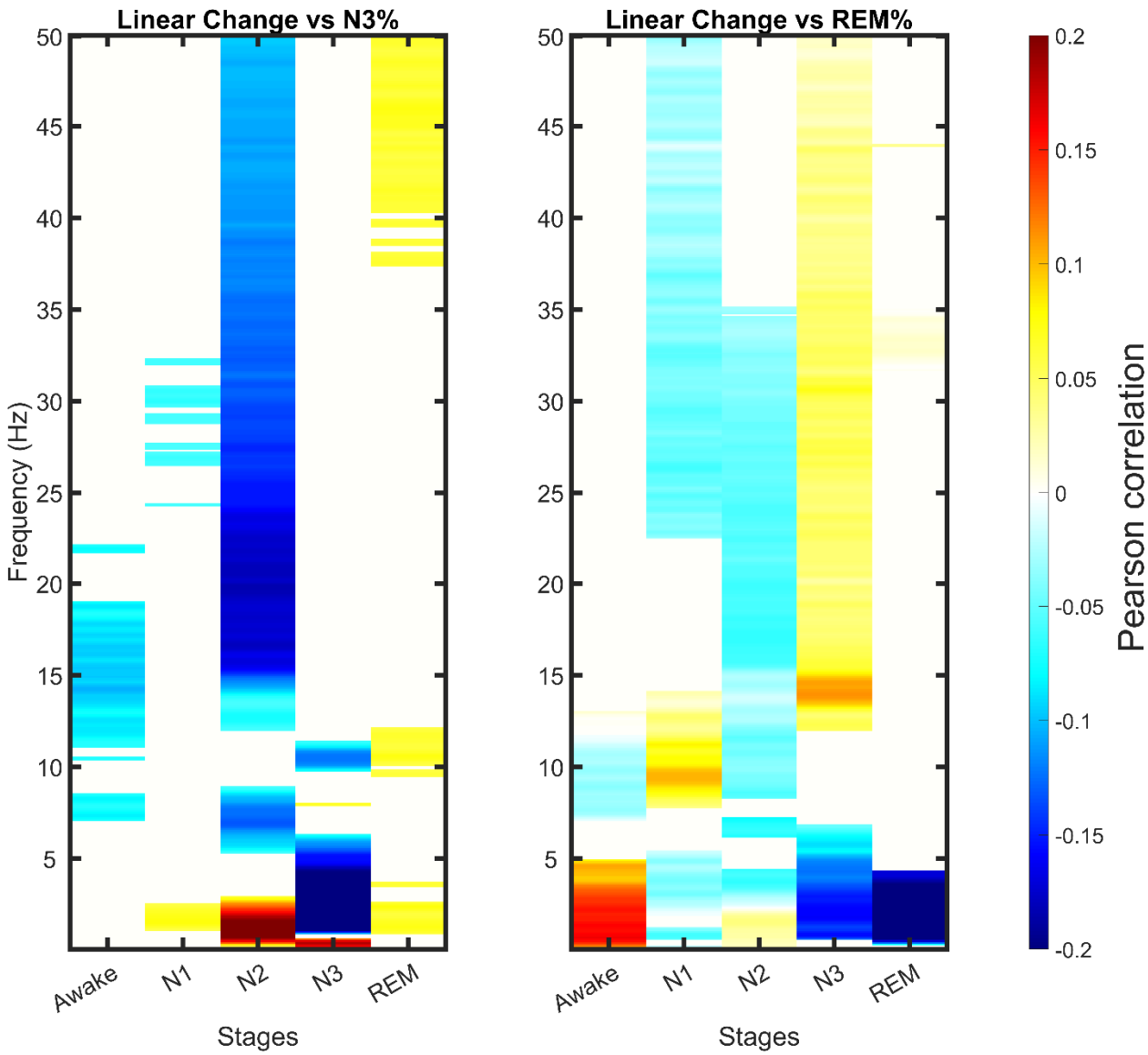

Figure 8. Correlation of temporally** regressed **spectral power with N3 percentage (left) and REM percentage (right) across sleep stages and frequencies.

Figure 8. This figure shows the results of correlations between temporally regressed spectral power and the percentage of N3 sleep (left) and REM sleep (right) for each sleep stage (awake, N1, N2, N3, and REM) and frequency range from 0.1 to 50 Hz. Warm colors (yellow to red) represent positive correlations, indicating that increases in spectral power over time are associated with higher N3 or REM percentages, while cool colors (cyan to blue) represent negative correlations. Statistically significant areas ($p < 0.05$, FDR-corrected) are colored.

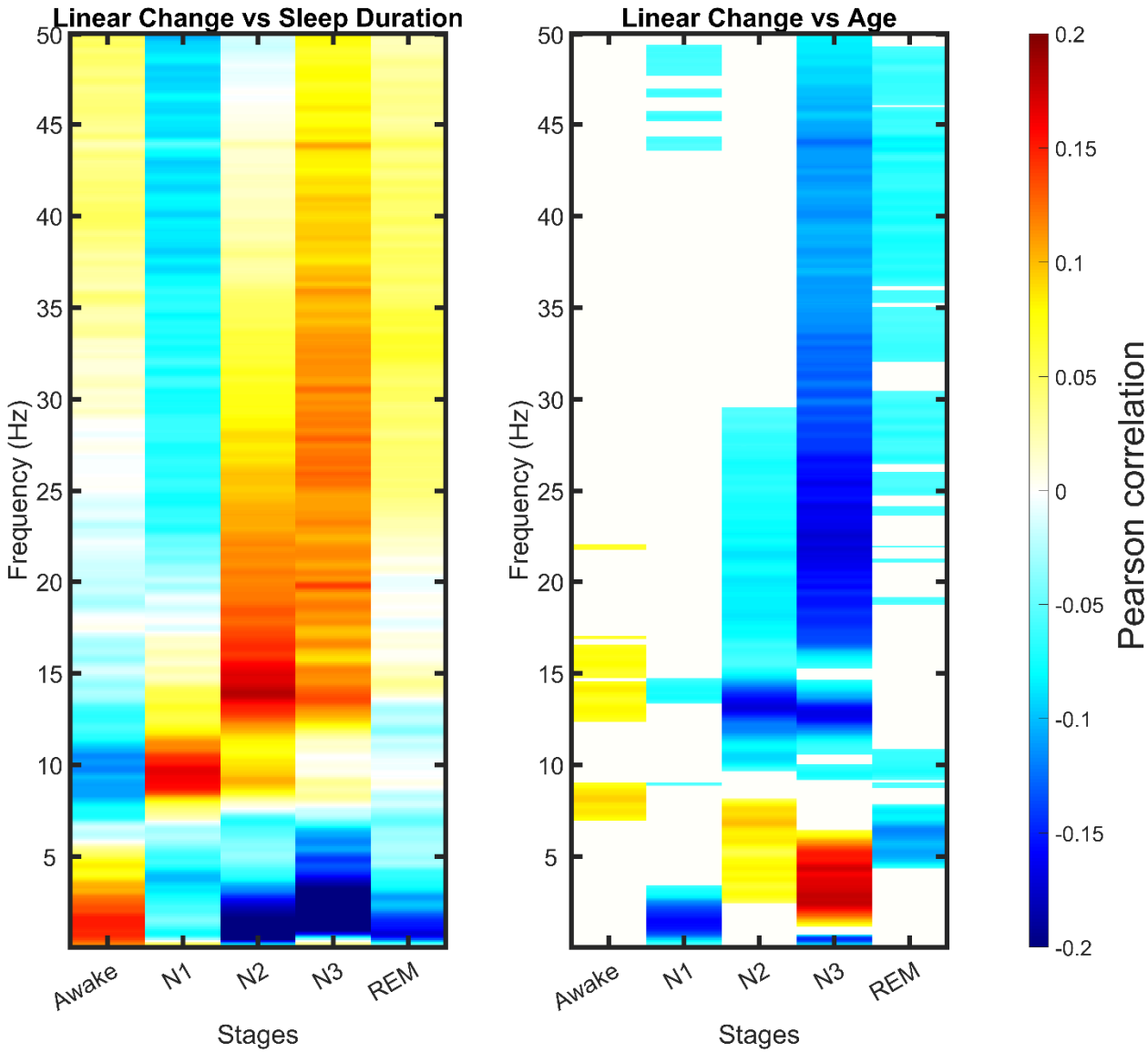

Figure 9. Correlation of temporally regressed spectral power with sleep duration (left) and age (right) across sleep stages and frequencies.

Figure 9. This figure illustrates the correlations between temporally regressed spectral power and total sleep duration (left) and age (right) for each sleep stage (awake, N1, N2, N3, and REM) and frequency range from 0.1 to 50 Hz. Warm colors (yellow to red) indicate positive correlations, showing that increases in spectral power over time are associated with longer sleep duration or greater age, while cool colors (cyan to blue) indicate negative correlations. Statistically significant regions ($p < 0.05$, FDR-corrected) are colored.

Discussion

This study provides a comprehensive analysis of EEG spectral power across different sleep stages and transitions therebetween, confirming established findings while offering novel insights that challenge current literature on sleep. By examining the relationships between EEG spectral power and key metrics—such as N3 percentage, REM percentage, total sleep duration, and age—both in static and temporally regressed forms, we have gained new perspectives on how sleep evolves over time and how brain activity relates to sleep quality and aging. The results highlight several important implications for the regulation of sleep, novel observations that contrast with previous findings, and potential applications for personalized sleep interventions, including brain-computer interfaces (BCIs).

Many of our results corroborate existing knowledge of sleep neurophysiology, particularly regarding transitions from wakefulness into NREM and REM sleep. The decrease in beta and gamma power (16–50 Hz) observed during the transition from wakefulness to N1 and N2 sleep stages reflects the brain's gradual disengagement from sensory input and cognitive processing as sleep deepens. This finding is consistent with several studies that have documented reductions in high-frequency activity during early sleep as an indicator of reduced cortical arousal (Cantero et al. 2004); (Cantero et al., 2004; Gais et al., 2007)(Iber et al. 2007).

Similarly, the observed increase in lower-frequency power—particularly in the delta (0.1–4 Hz) and theta (4–7 Hz) bands—as subjects transition from wakefulness into NREM stages, which mirrors the well-established pattern of increasing cortical synchronization in the early stages of sleep (Steriade, McCormick, and Sejnowski 1993)(Borbély & Achermann, 1999). These low-frequency oscillations are known to play a crucial role in early sleep stages, reflecting the brain's shift into a restorative state (D.-J. Dijk 2009).

Our findings also reaffirm the role of sigma power (12–15 Hz) in sleep spindle activity during N2 sleep, which is associated with sleep stability, memory consolidation, and cognitive processing (Fogel and Smith 2011); (Mölle et al. 2002)(. Consistent with earlier research, we observed that sleep spindle activity decreases during transitions from N2 to N3 (Figure 3), which reflects the reduction of spindle generation as the brain enters deep NREM sleep, dominated by slow-wave activity (SWA) (Andrillon et al. 2011).

The increase in delta power during N3 sleep, particularly in the very low delta range (0.1–0.4 Hz), further corroborates the established understanding of slow-wave sleep (SWS) as the most restorative stage of sleep. This finding aligns with the extensive literature demonstrating that slow-wave activity (SWA) is critical for neural recovery, memory consolidation, and overall brain plasticity during sleep (Tononi and Cirelli 2006); (Diekelmann and Born 2010). Additionally, the increase in both low-frequency (delta and theta) and high-frequency (beta and gamma) power during REM sleep is consistent with previous reports that REM is characterized by mixed-frequency EEG patterns, reflecting both high cortical arousal and periods of synchronization, which are crucial for emotional regulation and dreaming (Nir and Tononi 2010); (Insana 2020); (Llinás and Ribary 1993).

One of the most novel and surprising findings from this study is the inverse relationship between spectral power in multiple frequency bands and N3% across several sleep stages, including N1, N2, and REM. Previous research has consistently emphasized the importance of slow-wave activity (SWA), particularly delta power, as a marker of deep, restorative sleep (Tononi and Cirelli 2006)(Borbély & Achermann, 1999). However, our data suggest that reductions in spectral power across multiple frequencies, especially in sigma (12–15 Hz), beta (16–25 Hz), and gamma (25–50 Hz) ranges, are associated with higher N3%, indicating that lower brain activity during N1 and N2 may facilitate deeper sleep. This contrasts with existing studies that highlight the role of spindle activity in NREM sleep in enhancing slow-wave sleep (D.-J. Dijk 2009); (Fogel SM et al. 2007), suggesting a potential trade-off between spindle generation and the ability to enter deep sleep in some individuals.

The negative correlation between low delta power (0.1–0.5 Hz) during N2 and both N3% and total sleep duration (TST) is another surprising finding. Delta activity has long been considered essential for the restorative processes of sleep, particularly during N3 (Achermann and Borbély 1997); (Massimini et al. 2005), but its role during N2 is less understood. Our results suggest that excessive low-frequency power in N2 may hinder deeper sleep stages, potentially disrupting the balance between early-stage sleep and subsequent slow-wave sleep. This is consistent with previous discussions on the potential for excessive SWA during lighter NREM stages to disrupt

overall sleep architecture (Willi et al. 1998), challenging the traditional view that more delta activity is always beneficial. This novel finding adds nuance to the understanding of how different levels of delta power during early NREM stages affect transitions into deeper sleep.

The correlations between REM percentage and spectral power across different stages provide further insight. The weak but significant negative correlations between high-frequency activity (alpha to gamma) during NREM stages and REM% align with studies suggesting that excessive cortical activation can interfere with REM sleep (Bódizs et al., 2005). More interestingly, our finding that delta power during wakefulness positively correlates with REM% suggests that pre-sleep cortical downregulation may play an important role in promoting REM sleep. This observation adds a new dimension to our understanding of how pre-sleep brain states can influence subsequent sleep architecture (Borbély 1982). While much research has focused on slow-wave sleep, these findings indicate that pre-sleep brain activity, particularly in the delta band, may also modulate REM sleep regulation, a relatively underexplored area in sleep science.

Correlations Between Temporally Regressed Spectral Power and Sleep Metrics

The temporally regressed spectral power analysis provided even more detailed insights into the dynamic relationships between EEG spectral activity and sleep metrics. A key finding from this analysis is the strong positive correlation between N3% and increases in delta power over time during N2, indicating that the buildup of slow-wave activity over the night is crucial for deep sleep. This supports the widely accepted theory of sleep homeostasis, in which slow-wave activity reflects the brain’s recovery needs and increases in response to sleep pressure (Borbély 1982); (Riedner et al. 2007). Similarly, the negative correlation between decreases in delta power during N3 and increases in N3% suggests that individuals who lose slow-wave activity too early might require more deep sleep overall. These results partially align with earlier work showing that the timing and maintenance of slow-wave activity are critical for the restorative function of sleep (Mander, Winer, and Walker 2017); (Massimini et al. 2004).

The results for REM% are also noteworthy. Temporal increases in delta power during the awake period positively correlated with REM%, suggesting that individuals who exhibit stronger cortical downregulation before falling asleep are more likely to experience higher amounts of REM sleep. This finding supports the idea that pre-sleep brain states play a critical role in determining sleep quality and the balance of sleep stages (Borbély et al. 1981). Moreover, the negative correlation between decreases in delta power during N3 and REM% suggests that increasing slow-wave activity over time may decrease the amount of REM, which has not been explored directly and reported in the literature.

The correlations between temporally regressed spectral power and sleep duration also provided interesting results. Temporal increases in delta power during the awake period were associated with longer total sleep time (TST), which is consistent with earlier findings showing that pre-sleep cortical downregulation is predictive of better sleep quality and longer sleep duration (Borbély et al. 1981); (D. J. Dijk et al. 1991)(Dijk et al., **1995**). On the other hand, reductions in delta power over time during N2 and N3 stages were associated with more TST, reinforcing the idea that the quality of deep sleep can lead to more efficient sleep throughout the night by requiring less of it. These results provide strong evidence for the role of slow-wave activity in regulating overall sleep architecture and duration (D.-J. Dijk 2009); (Tononi and Cirelli 2006).

Finally, the correlations between temporally regressed spectral power and age highlight the age-related decline in slow-wave dynamics. Our results show that delta power in N3 decreases over time in younger individuals and increases over time or potentially remains the same in older individuals, which overlaps with previous reports that aging is associated with a disruption of optimal slow wave activity and dynamics (Mander, Winer, and Walker 2017); (Ohayon et al. 2004). The decrease in power across various frequencies (very low delta, sigma, beta, and gamma) over time during N3 as it corresponds to older age goes against reports that aging individuals exhibit greater cortical activation during sleep, which may contribute to increased sleep fragmentation and reduced sleep efficiency (Carrier et al. 2001); (Feinberg and Campbell 2010). These findings suggest that interventions aimed at sustaining slow-wave activity during N3 could help improve sleep quality in older adults, who often suffer from sleep fragmentation and shorter periods of restorative sleep (Mander, Winer, and Walker 2017).

The findings from this study have important implications for sleep research and clinical practice. First, the novel observation that lower levels of spectral power during N1 and N2 are associated with increased N3% suggests that interventions aiming to reduce high-frequency brain activity in early sleep stages could promote deeper sleep. These insights could be used to develop personalized sleep therapies targeting specific frequency bands to improve sleep architecture.
One of the most promising applications of these findings is in the development of non-invasive brain-computer interfaces (BCIs) for sleep modulation. Sensory brain stimulation seems particularly promising for these purposes. BCIs that monitor EEG spectral power in real-time could be used to detect deviations from optimal sleep architecture and deliver interventions to correct them. For example, our findings suggest that BCIs could be programmed to detect excessive sigma or beta activity during N1 or N2 and provide neurofeedback or non-invasive stimulation to promote cortical downregulation, facilitating transitions into deeper sleep. Auditory or electrical stimulation targeted to enhance slow-wave activity during sleep has been shown to improve sleep quality and memory consolidation (Ngo et al. 2013); (Marshall et al. 2006), and these technologies could be further optimized using insights from spectral power dynamics.

In addition, BCIs could be designed to provide real-time feedback during the awake period to promote cortical downregulation before sleep, thereby enhancing REM sleep and overall sleep quality. By tracking pre-sleep delta power, BCIs could deliver feedback to help individuals achieve more optimal brain states for sleep onset, improving both sleep duration and stage transitions (Borbély et al. 1981); (Riedner et al. 2007). This could be particularly useful for individuals with insomnia or other sleep disorders, where disruptions in the balance of spectral power across sleep stages are common.

Furthermore, our findings on the relationship between spectral power and age suggest that BCIs could be used as diagnostic tools for detecting early signs of sleep deterioration in aging populations. By monitoring delta and gamma power dynamics across the night, BCIs could help identify age-related declines in sleep quality and provide personalized interventions to counteract these effects, such as stimulation to prolong slow-wave activity in N3 sleep. Such interventions

could mitigate the cognitive and physical declines often associated with poor sleep in older adults (Mander, Winer, and Walker 2017).

Limitations

Several limitations of this study should be noted, particularly in relation to the generalizability of the findings and the methodologies employed. First, while the sample size of 1137 participants provides a robust dataset, there are inherent limitations in the diversity of the sample that may affect the generalizability of the results. Factors such as age, health status, and individual sleep habits were not fully controlled, which may limit the application of these findings to broader populations. For example, although age was considered, other variables like medication use, lifestyle factors, or undiagnosed conditions could have influenced the EEG patterns and the relationships observed between spectral power and sleep metrics.

Another important limitation is the cross-sectional nature of the study. By relying on single-night EEG recordings, the study provides only a snapshot of each participant's sleep patterns. This design limits the ability to infer long-term trends or causal relationships, particularly with regard to age-related changes in sleep architecture. Longitudinal studies tracking changes in spectral power and sleep metrics over time are necessary to establish how sleep evolves and how factors like aging or lifestyle interventions might influence these dynamics.

Finally, the use of correlation analyses in this study limits the ability to draw firm conclusions about causality. While significant associations between spectral power and sleep metrics were observed, it remains unclear whether these spectral changes cause better sleep or if they are simply correlated with other underlying processes. Future studies that involve experimental manipulations, such as using neurostimulation to modulate specific frequency bands, could help determine the causal relationships between brain activity and sleep quality.

Future Directions

To build on the findings of this study, future research should aim to integrate additional physiological and behavioral metrics alongside EEG spectral power analysis. Incorporating measures such as heart rate variability, respiration, and hormonal data, as well as cognitive performance assessments, would provide a more comprehensive understanding of how brain activity during sleep influences overall health and daytime functioning. These combined measures would allow researchers to explore the complex interactions between sleep, physiology, and behavior in greater depth.

Experimental manipulations, such as using non-invasive brain stimulation techniques like transcranial electrical stimulation (tES), deep brain magnetic stimulation (DBMS) or sensory (visual and/or auditory) brain stimulation, could help establish causal relationships between spectral power and sleep quality. These interventions would offer insights into how specific frequency bands, such as slow-wave activity or sleep spindles, contribute to sleep architecture and could be used to develop targeted therapies for improving sleep in clinical populations.

Finally, future research should expand to cross-cultural and population-based studies to examine how different environments, lifestyles, and stressors influence sleep architecture and spectral dynamics. This would provide a broader understanding of sleep variability across populations and could inform public health strategies aimed at improving sleep and preventing sleep-related health issues on a global scale.

Conclusion

In summary,(n.d.) this study provides a detailed analysis of EEG spectral power across different sleep stages and transitions, revealing both established findings and novel insights. We confirmed known patterns such as the decrease in high-frequency power during transitions to NREM sleep and the increase in low-frequency power during deep sleep, while also identifying unexpected inverse correlations between spectral power and N3 percentage, suggesting that lower brain activity in earlier stages facilitates deeper sleep. Additionally, the relationships between spectral power and key metrics like REM percentage, sleep duration, and age offer new perspectives on how sleep quality is regulated and declines with aging. The results highlight the

potential for personalized sleep interventions using brain-computer interfaces (BCIs) that monitor and modulate spectral power in real-time to optimize sleep architecture and improve overall health. These findings open the door for future research to explore causal relationships and develop targeted therapies for sleep enhancement.

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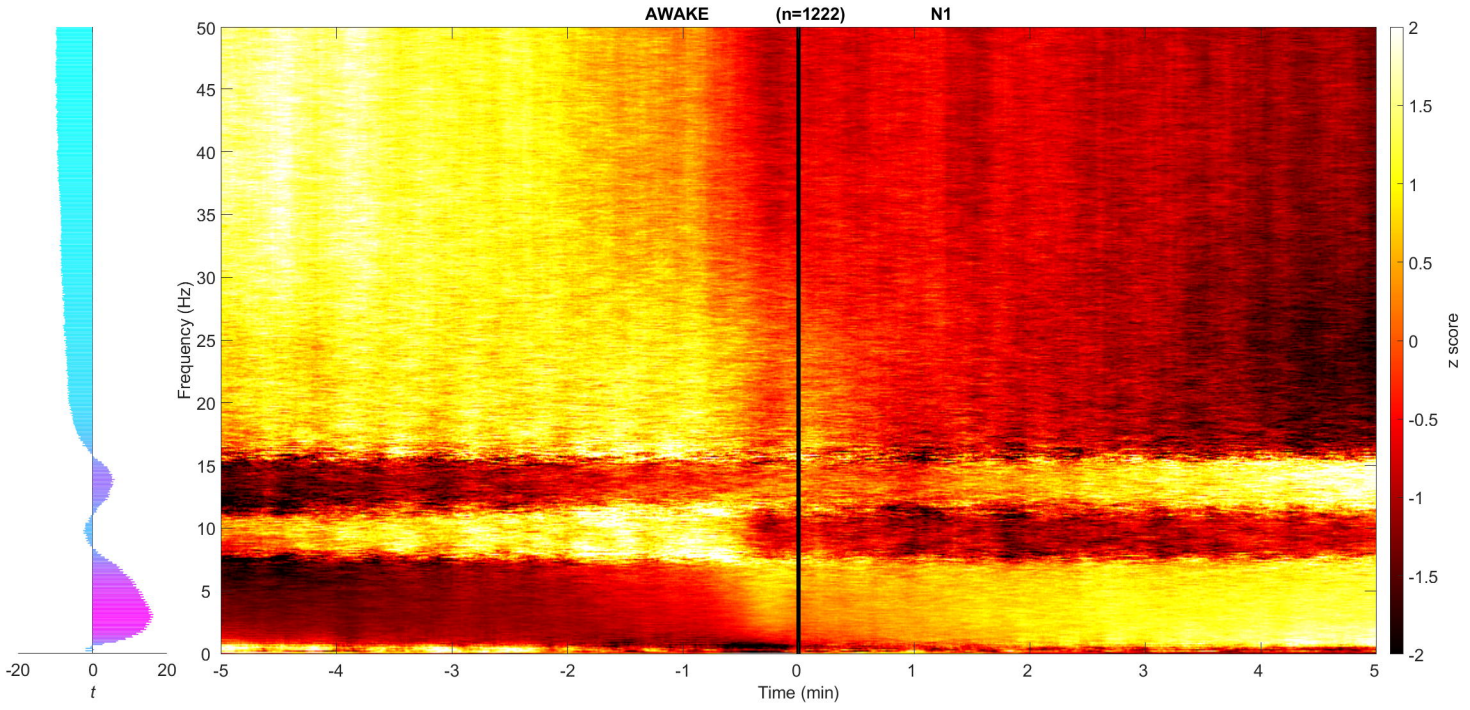
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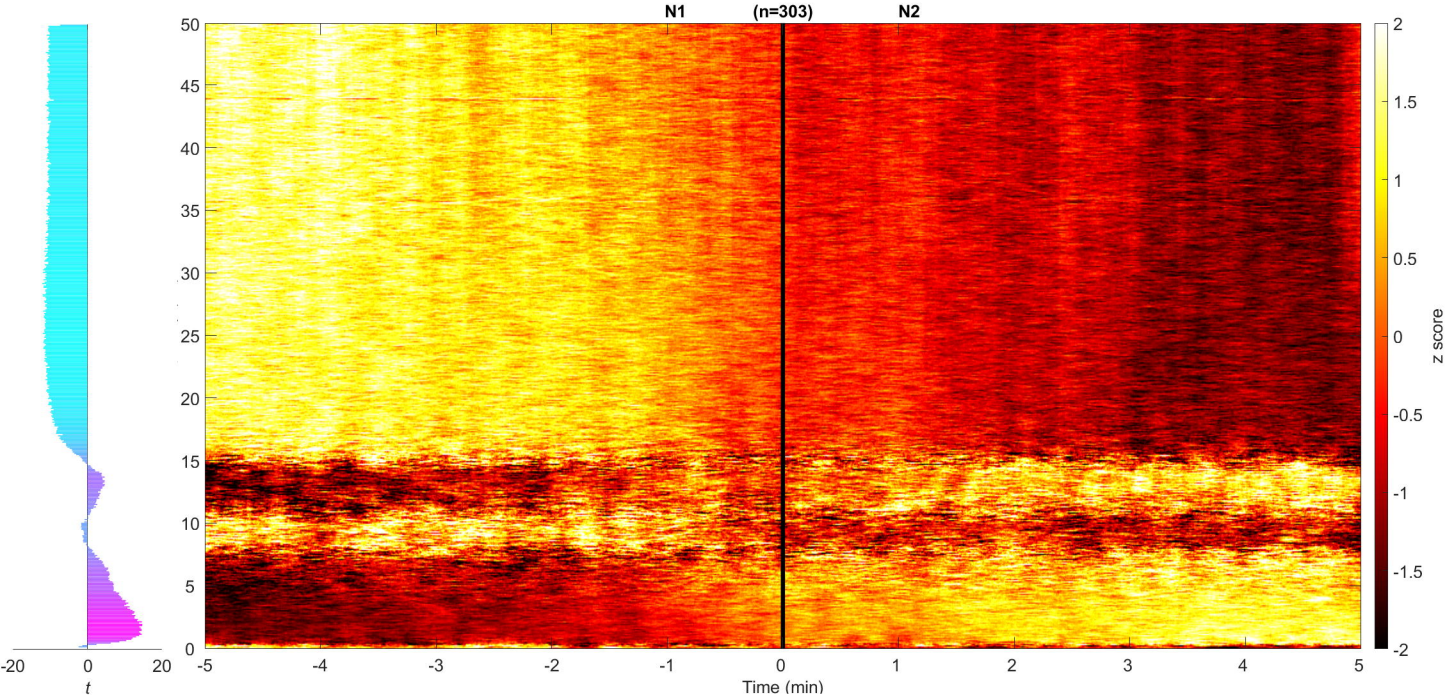
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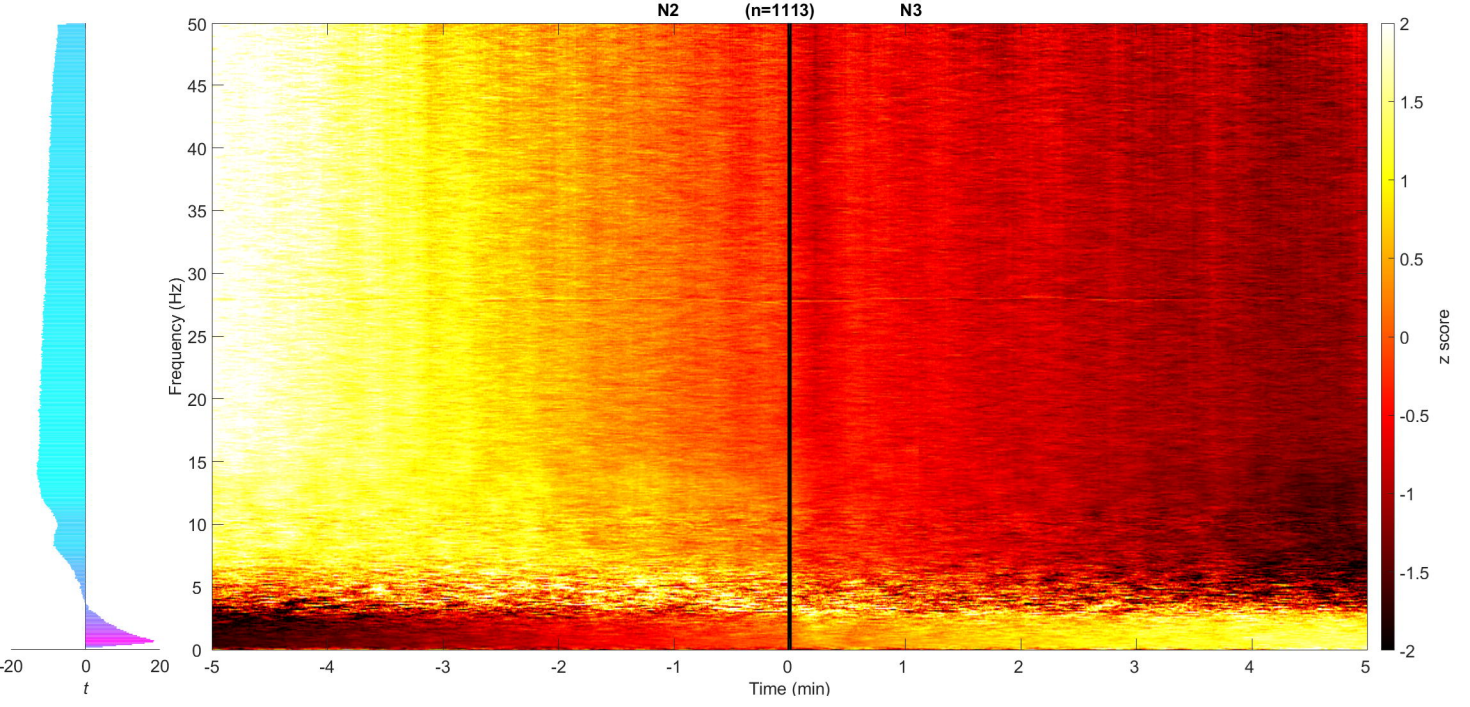
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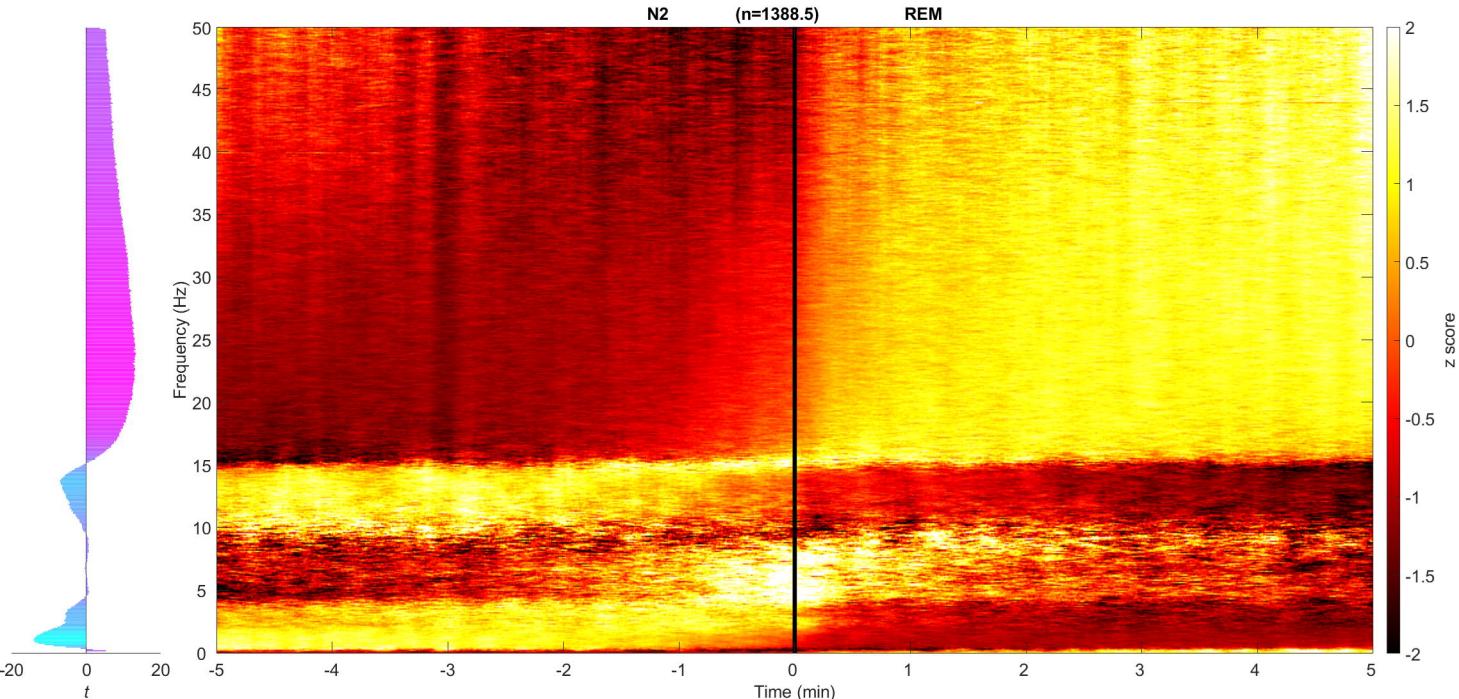
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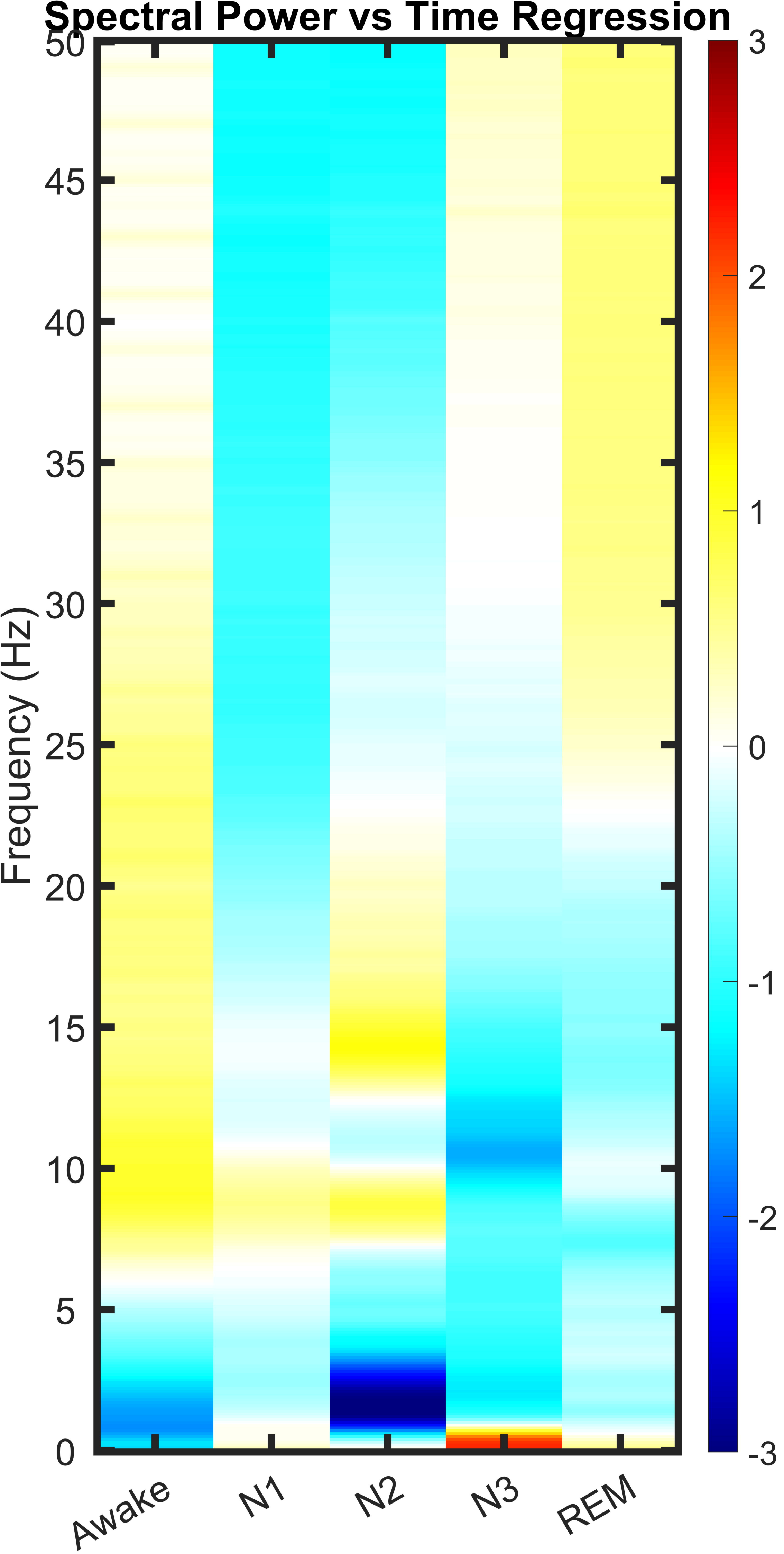
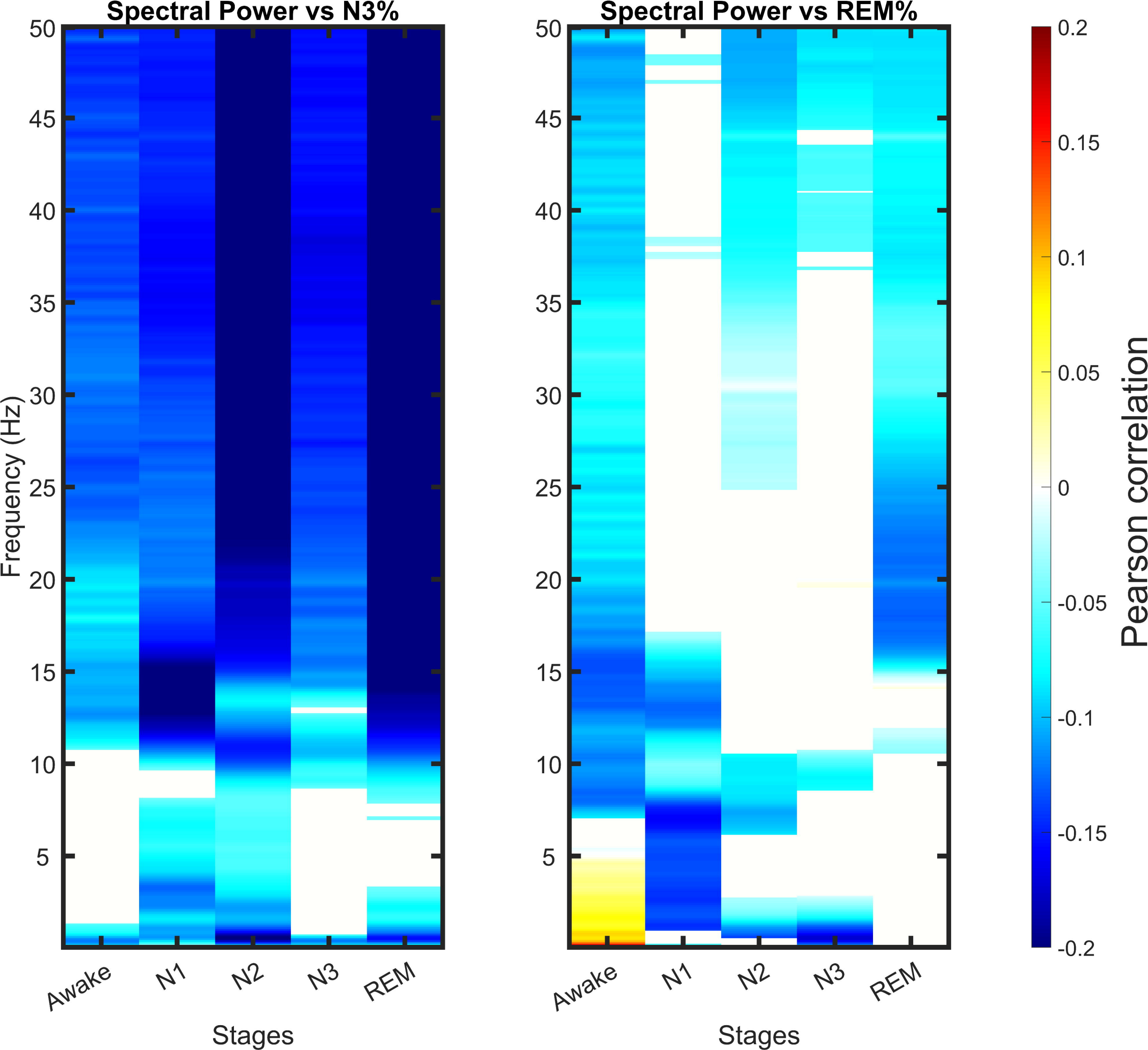
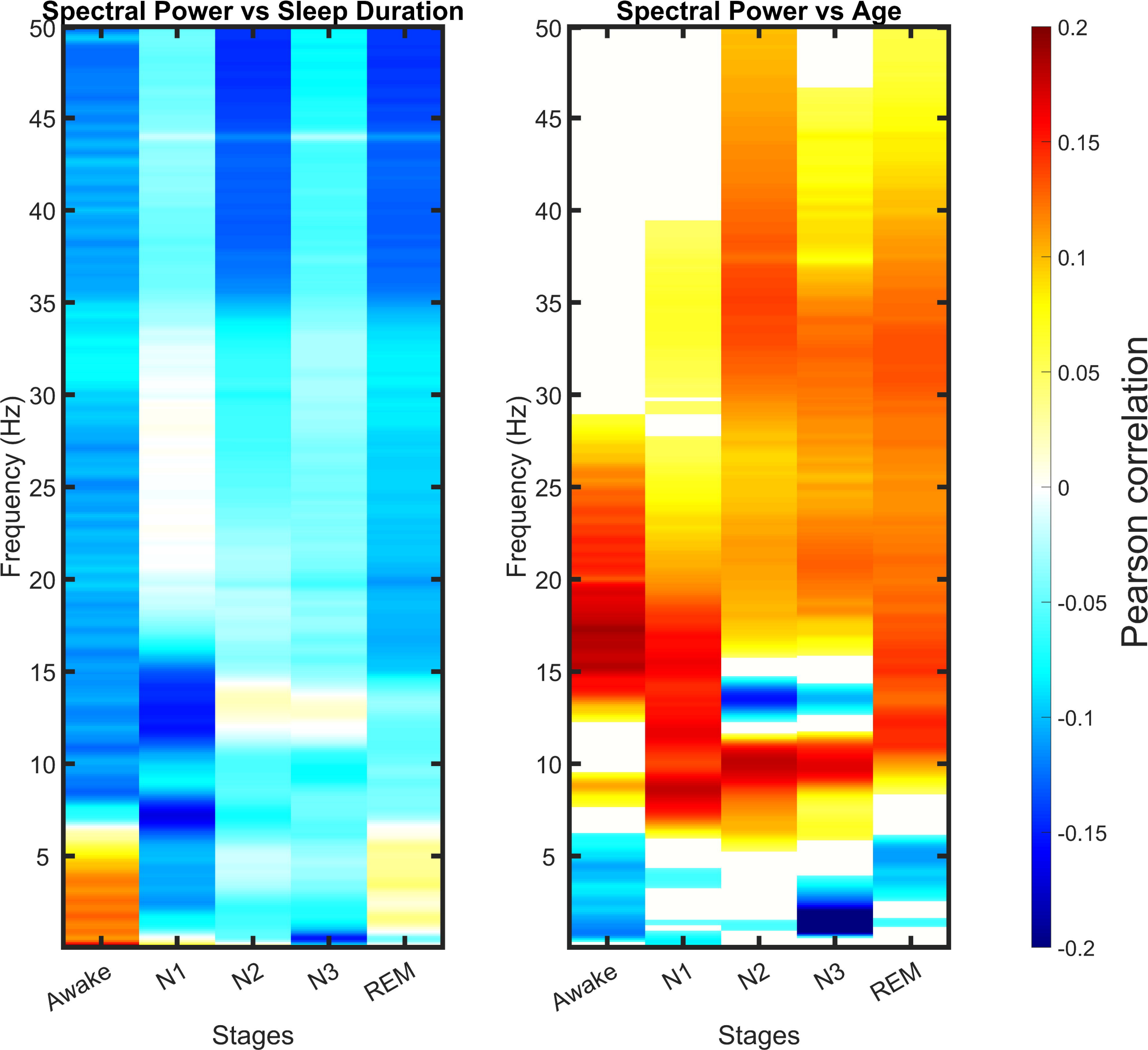
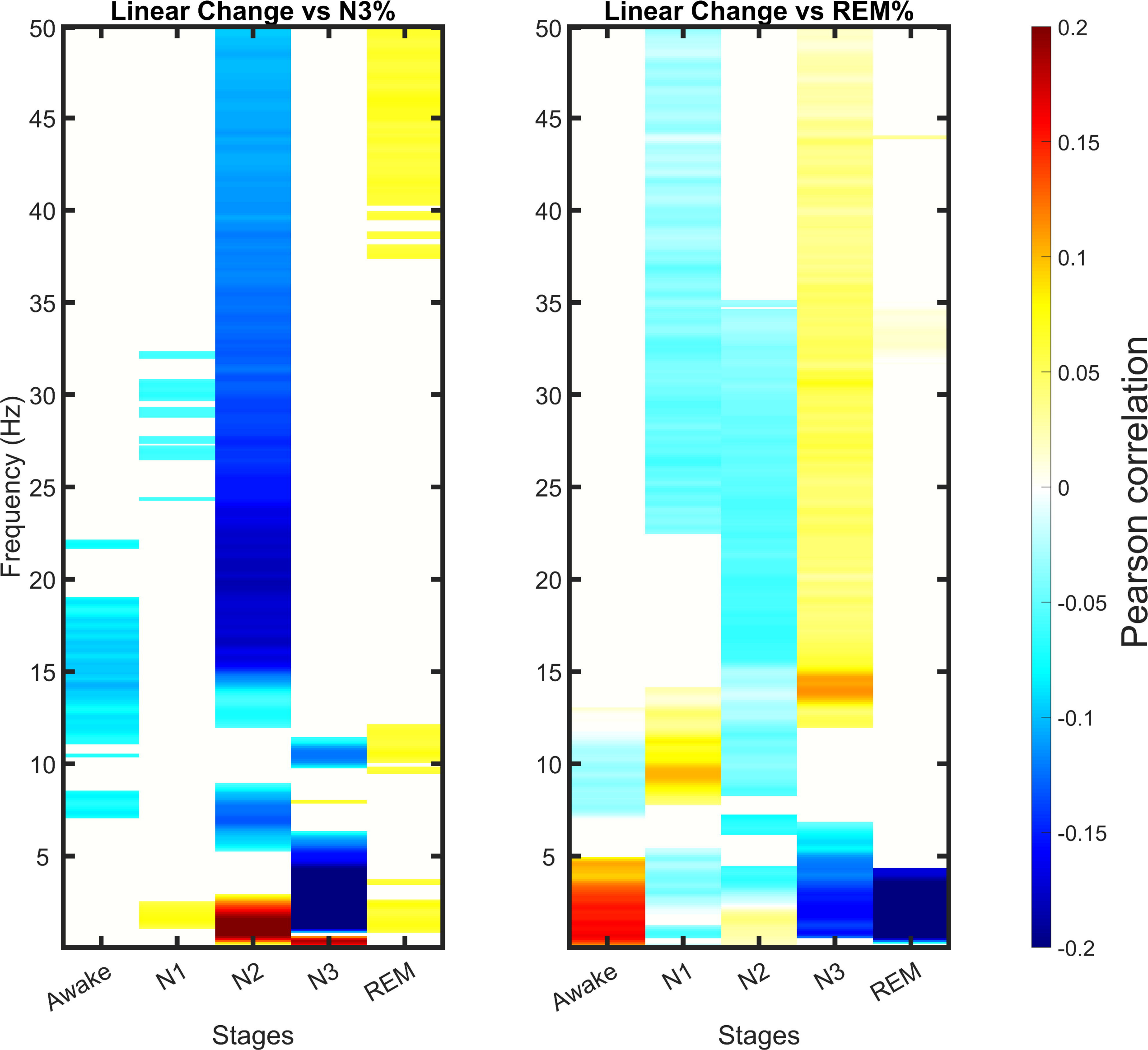
20
-5
-4
-3
-2
-1
0
1
2
3
4
5
0
5
10
15
20
25
30
35
40
45
50
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2

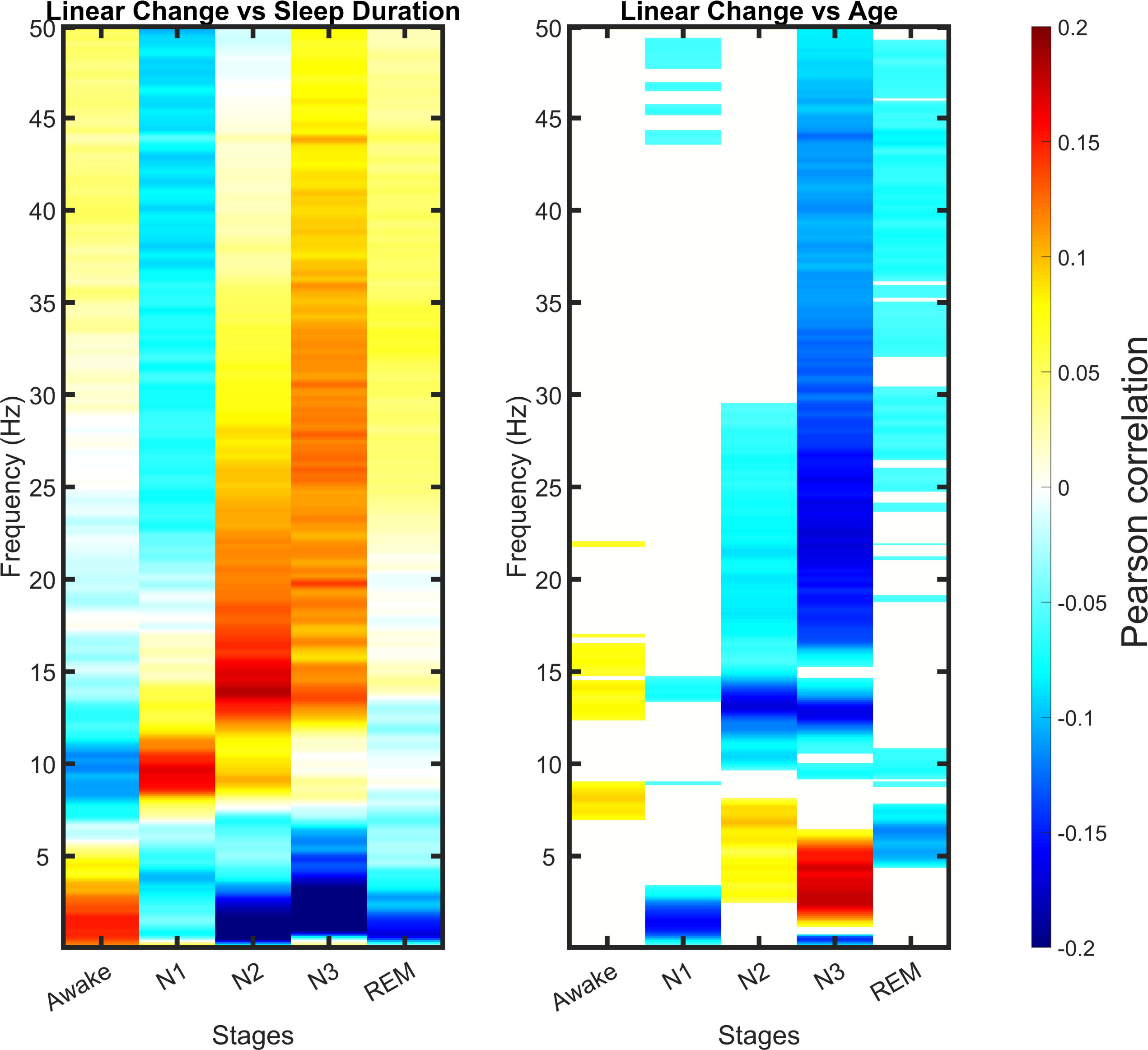
Spectral Power vs Time Regression




Spectral Power vs N3%
Spectral Power vs REM%
Frequency (Hz)
50
45
40
35
30
25
20
15
10
5
Awake
N1
N2
N3
REM
Stages
Pearson correlation
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.2


Spectral Power vs Sleep Duration
Spectral Power vs Age
Frequency (Hz)
50
45
40
35
30
25
20
15
10
5
Awake
N1
N2
N3
REM
Stages
Pearson correlation
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.2


Linear Change vs N3%
Linear Change vs REM%
Frequency (Hz)
50
45
40
35
30
25
20
15
10
5
Awake
N1
N2
N3
REM
Stages
Pearson correlation
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.2


Linear Change vs Sleep Duration
Linear Change vs Age
Frequency (Hz)
50
45
40
35
30
25
20
15
10
5
Awake
N1
N2
N3
REM
Stages
Pearson correlation
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.2