Dissociating Contributions of Theta and Alpha Oscillations from Aperiodic Neural Activity in Human Visual Working Memory

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Code and Data availability

All data used in this study are publicly available at:
https://osf.io/8xuk3/
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All code used for all analyses and plots are publicly available on GitHub at:
https://github.com/voytekresearch/WM_specparam

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Author contributions

Q.v.E., K.A., T.D., and B.V. conceived of the experiments and contributed to the intellectual and methodological development of the ideas. Q.v.E., G.C., A.S., and T.D. wrote analysis code and analyzed data. Q.v.E., K.A., T.D., and B.V. wrote and edited the manuscript.

Competing interests

The authors declare no competing interests.

Abstract

While visual working memory (WM) is strongly associated with reductions in occipitoparietal 8-12 Hz alpha power, the role of 4-7 Hz frontal midline theta power is less clear, with both increases and decreases widely reported. Here, we test the hypothesis that this theta paradox can be explained by non-oscillatory, aperiodic neural activity dynamics. Because traditional time-frequency analyses of electroencephalopgraphy (EEG) data conflate oscillations and aperiodic activity, event-related changes in aperiodic activity can manifest as task-related changes in apparent oscillations, even when none are present. Reanalyzing EEG data from two visual WM experiments (n = 74), and leveraging spectral parameterization, we found systematic changes in aperiodic activity with WM load, and we replicated classic alpha, but not theta, oscillatory effects after controlling for aperiodic changes. Aperiodic activity decreased during WM retention, and further flattened over the occipitoparietal cortex with an increase in WM load. After controlling for these dynamics, aperiodic-adjusted alpha power decreased with increasing WM load. In contrast, aperiodic-adjusted theta power increased during WM retention, but because aperiodic activity reduces more, it falsely appears as though theta “oscillatory” power (e.g., bandpower) is reduced. Furthermore, only a minority of participants (31/74) had a detectable degree of theta oscillations. These results offer a potential resolution to the theta paradox where studies show contrasting power changes. We identify novel aperiodic dynamics during human visual WM that mask the potential role that neural oscillations play in cognition and behavior.

Significance statement (120)

Working Memory (WM) is our ability to hold information in mind without it being present in our external environment. Years of research focused on oscillatory brain dynamics to discover the mechanisms of WM. Here, we specifically look at oscillatory and non-oscillatory, aperiodic activity as measured with scalp EEG to test their significance in supporting WM. We challenge earlier findings regarding theta oscillations with our analysis approach, while replicating alpha oscillation findings. Furthermore, aperiodic activity is found to be involved in WM, over frontal regions in a task-general manner, and over anterior regions this activity is reduced with an increase the number of items that are remembered. Thus, we have identified novel aperiodic dynamics during human visual WM.

1. Introduction

We commonly encounter situations where we need to remember the color and identity of objects in our environment, ranging from simple tasks like cooking, to the games we play, to more complex interactions with our environment. Visual working memory (WM) refers to our ability to actively maintain information in mind, for a brief period of time, that is used to guide behavior to execute these tasks (Baddeley, 1992; D’Esposito & Postle, 2015). It is characterized by its limited capacity (Cowan, 2010; Miller, 1956; Oberauer et al., 2016).

Using electroencephalography (EEG), systematic changes in neural activity have been observed while participants maintain items in memory, even in the absence of continuing sensory input. In particular, two oscillatory bands have been identified as playing an important role in WM: frontal midline theta (4-7Hz, hereafter just “theta”) (Berger & Sauseng, 2022; Hsieh & Ranganath, 2014; Jensen & Tesche, 2002), and occipitoparietal alpha (8-12Hz, hereafter, “alpha”) (D’Esposito & Postle, 2015; Gevins & Smith, 2000; Halgren et al., 2002; Pavlov & Kotchoubey, 2022). Decreases in alpha power have been widely observed with increasing WM load (Fukuda et al., 2015, 2016), whereas hemispheric differences due to load have inconsistent findings (Adam et al., 2018, 2020; Medendorp et al., 2007; Sauseng et al., 2009; van der Werf et al., 2008; van Dijk et al., 2010). Topographical changes in alpha power can be used to decode the location of items in WM (Bae & Luck, 2018; Foster et al., 2016). In contrast, theta's role in

WM is less clear, with studies reporting a mix of WM-related power increases and decreases, even within the same study (Herweg et al., 2020; Pavlov & Kotchoubey, 2022).

This lack of clarity regarding the role of theta might be explained by non-oscillatory, aperiodic neural dynamics. Traditional time-frequency analysis methods – including wavelet analysis, and the filter-Hilbert approach – conflate neural oscillations with non-oscillatory, aperiodic activity (Donoghue, Haller, Peterson, et al., 2020; He, 2014). Historically often treated as task-irrelevant noise, there is a growing consensus that aperiodic activity is dynamic and task-relevant, with recent research highlighting its role in aging (Voytek et al., 2015), sleep (Höhn et al., 2024; Lendner et al., 2020), anesthesia (Colombo et al., 2019; Waschke et al., 2021), and disease (Helson et al., 2023; Karalunas et al., 2022; Smith, Kosik, van Engen, et al., 2023; Smith, Ma, et al., 2023). Preliminary evidence suggests that resting-state aperiodic activity is correlated with WM capacity (McKeon et al., 2024), and task-based aperiodic activity is functionally relevant in WM processes (Frelih et al., 2024; Gyurkovics et al., 2022; Virtue-Griffiths et al., 2022).

Here, we tested the hypothesis that mixed results regarding theta in human WM can potentially be resolved by accounting for event-related aperiodic dynamics. While it is possible the same applies to occipitoparietal alpha activity - it might be driven, in whole or in part, by aperiodic activity - previous work suggests that alpha oscillations, due to typically having higher power, are less likely to be masked by aperiodic dynamics than theta (Donoghue, Dominguez, et al., 2020). We illustrate three scenarios where task-induced changes to the neural power spectrum appear as theta bandpower decreases (**Fig. 1C**). The first scenario illustrates the - potentially incorrectly - standard model, whereby aperiodic activity is stable between task-states while narrowband theta oscillatory power dynamically changes. The second and third scenarios show no difference in relative oscillatory theta power (peak height), even though total theta bandpower decreases relative to baseline. Here, theta band effects are driven by aperiodic dynamics, regardless of whether detectable theta oscillations are present.

Here we reanalyzed two large (n = 74) human EEG datasets of participants performing a visual WM task (**Fig. 1A**) (Adam et al., 2018). Using spectral parameterization (**Fig. 1B**), we replicated traditional alpha effects even when accounting for aperiodic activity; power decreased with increasing WM load. The original paper used the filter-Hilbert method and reported task-related theta power decreases during WM retention. In contrast, we found aperiodic-adjusted theta power increased during retention, but a simultaneous decrease in aperiodic activity overwhelmed this relatively smaller theta oscillatory power increase. To traditional analysis methods it would appear as though theta power reduced when, in fact, the opposite occurred.

By disentangling aperiodic activity from narrowband oscillations, we found aperiodic activity dynamically decreases (spectral flattening) due to task-general demands in the frontal midline and occipitoparietal regions. This effect was task-dependent in occipitoparietal regions, with a higher reduction in aperiodic activity with increased WM load. Consistent with prior research (Bailey et al., 2020; Klimesch, 1999; Mitchell et al., 2008), we found evidence for theta oscillatory activity in less than half (42%) of the participants, whereas almost every participant (91%) showed clear alpha oscillatory activity. Our results demonstrate how implicit assumptions of our analysis methods can yield misleading conclusions. While theta oscillations clearly play a role in rodent hippocampal function relating to behavioral and cognitive tasks (Soltani Zangbar et al., 2020; Vanderwolf, 1969), the evidence for human frontal midline theta is more sparse and mixed (Herweg et al., 2020; Pavlov & Kotchoubey, 2022). Not only did our findings show correlational evidence of aperiodic activities involvement in human visual WM, we also demonstrated new insights into oscillatory dynamics by accounting for event-related aperiodic activity.

2. Methods

2.1. Study design from Adam et al. (2018)

All data used in this manuscript was obtained from OSF (https://osf.io/8xuk3/) (Adam et al., 2018).

2.1.1. Participants

Unique participants were recruited for Experiments 1 and 2. All participants were between the age of 18 and 35, with normal or corrected-to-normal visual acuity and color vision. Data from 31 participants were collected in Experiment 1, and 48 participants in Experiment 2. For more details on inclusion and exclusion criteria, see Adam et al. (2018). After EEG artifact rejection, 30 participants were considered for further analysis in Experiment 1, and 44 in Experiment 2.

2.1.2 Task design

In both experiments, participants performed a whole-report visual WM task (**Fig. 1A**), in which they were asked to remember the colors of differently colored squares across a blank screen retention period and then recall the colors of all remembered items (Huang et al 2010; Adam et al, 2015). Throughout each trial, participants were asked to fixate on a dot presented in the middle of the screen, except during the response. A cue was presented for 1100 ms to indicate whether they had to memorize the items on the right or the left side of the screen. The memory array was presented for 250 ms followed by a retention period of 1300 ms, after which a response for each cued item had to be given (**Fig. 1B**). The number of items were equal on each side to balance the visual stimulation within each visual hemifield. This design was chosen to ensure hemispheric differences in neural activity were driven by cognitive demands, rather than perceptual demands (Vogel & Machizawa, 2004).

Each block consisted of 30 trials. For Experiment 1, each block had 10 trials for three different set sizes, one, three or six, and Experiment 2 contained 30 trials of set size six. The conditions in Experiment 1 were defined as the three set sizes, whereas in Experiment 2 two conditions were defined based on the performance on each trial: if more than three items were correctly answered, it was deemed a “high performance” trial, versus having less than three items correct was deemed a “poor performance” trial.

2.1.3 EEG measurements

EEG passive electrodes and cap were from ElectroCap International (Eaton, OH). Recordings were done on an SA Instruments Amplifier running LabView 6.1 (Fife, Scotland). The cap contains 20 electrodes according to the 10/20 international sites. Two supplementary electrodes were placed over the occipital lobe: OL was placed between T5 and O1, and OR was placed between T6 and O2. In addition, electrooculography (EOG) was recorded to measure horizontal eye movements and blinks. For more detailed information (Adam et al., 2018; Foster et al., 2016).

2.1.4 EEG preprocessing

Data were available from the original paper’s repository, already pre-processed and epoched, but not baselined. Pre-processing steps included: automatic removal of trials with eye blinks or eye movements using a set threshold, automatic removal of trials with excessive noise using a peak-to-peak threshold rejection, and finally a visual inspection of the data to determine whether the automated steps were successfully implemented. More details can be found in Adam et al. (2018). Here, we used the non-baselined epochs.

The same electrode clusters were used as defined by the original paper (Adam et al., 2018) for replicating their original results, and the novel analysis conducted in this paper. These clusters for lateralized alpha were left and right occipital and parietal regions (O1, OL, P3, PO3, T5, O2, OR, P4, PO4, and T6), and for theta a cluster over the frontal-midline (F3, F4, Fz).

2.2 Replication of original results

A detailed description of the replication methods and results can be found in the Jupyter notebooks hosted at GitHub.

To replicate the original results we performed separate bandpass filtering in the theta (4-7Hz) and alpha (8-12Hz) bands. We then performed a Hilbert transform to compute the analytic amplitude of these frequency bands over time. This amplitude was baseline corrected to 400 ms before cue onset.

For statistical analysis, theta and alpha power was averaged over the retention period (400 - 1500 ms after memory array onset) per condition per the original approach. A two-way repeated-measures ANOVA was performed on alpha power with condition (set size for Experiment 1 or performance for Experiment 2) and lateralization as factors. Note that the factor set size or performance is comparable to a whole-field alpha approach, and the second factor adds the lateralization effect. A pairwise t-test was used on theta power to investigate the difference between good and poor performance.

2.3 Spectral parameterization: separating oscillatory from aperiodic activity

2.3.1 The specparam model

Spectral parameterization (Donoghue, Haller, Peterson, et al., 2020) models a power spectrum as a combination of an aperiodic component (fit as a Lorentzian) and putative oscillatory components that rise above the aperiodic signal (fit as Gaussians). Here, the parameters characterizing the aperiodic component are the spectral exponent and the offset. Three parameters characterize the Gaussian periodic components: peak height (relative to the aperiodic signal), center frequency, and bandwidth (**Fig. 1B**). More details can be found in (Donoghue, Haller, Peterson, et al., 2020).

2.3.2 Identification of participants exhibiting oscillatory activity

Because oscillations are not consistently present (Jones, 2016), spectral parameterization helps to explicitly identify participants and electrodes where there are putative oscillations (defined here as having a significant "bump" in the power spectrum within the theta or alpha range above aperiodic activity). This triggered an additional inclusion criterion, different from the original report, in that oscillatory activity should only be analyzed from participants who exhibited putative oscillations. Thus, for alpha power in Experiments 1 and 2, participants were required to have a parameterized spectral peak between 8 and 12 Hz in the occipitoparietal electrodes. For theta power, participants were required to have a peak between 4 and 7 Hz that was distinct from alpha activity on frontal midline electrodes (detailed below). To perform this analysis, a power spectrum was generated for every trial, for the whole trial length using Welch's method and a Hanning window of two times the sampling frequency (2*250 samples). The model was applied to the power spectrum in the frequency range of 2-40 Hz. Peak width limits were set from 2-8 Hz. To minimize overfitting of relatively flat spectra without peaks, *specparam* requires an amplitude threshold for determining the height of the Gaussian, relative to the aperiodic signal, to be considered a peak. This threshold was set at 0.2 μV^2/Hz for the alpha frequency band, and 0.1 μV^2/Hz for theta frequency band. Different absolute thresholds were chosen for the bands because theta power is typically lower than alpha power, relative to the aperiodic fit. For both experiments, *specparam* successfully discriminated between participants who exhibited alpha power and those who did not. This was further confirmed by visual inspection. However, discriminating participants based on theta power proved to be more difficult because not all participants exhibited a distinct theta peak. A portion of participants also exhibited alpha power on the frontal midline electrodes overlapping with the theta frequency range. Therefore, determining whether a participant exhibits theta power was guided by *specparam* and confirmed with manual visual classification to avoid lower frequency alpha peaks to be considered theta.

2.3.3 Generating single trial power spectra and applying specparam

A power spectrum was created for each trial, for all electrode groups – contralateral occipitoparietal, the ipsilateral occipitoparietal, and frontal midline. The same electrodes were used as in the replication results. A time window from 400 to 1500 ms after memory array onset (1100 ms) was used for the retention period to produce power spectra, excluding the early perceptual ERP time points (Kałamała et al., 2024). For the baseline period, we used the cue period from -1100 until memory array onset (1100 ms). This decision is due to the ITI only being 500 ms long. Power spectra were created using Welch's method and a Hanning window that was equal to the length of the data (1100 ms).

The *specparam* model was applied to these power spectra using the same settings described in section 2.2.3. Four outputs were collected:

1) The peak height within a frequency range of 8 to 12 Hz for alpha power and 4 to 7 Hz for theta power, for both the retention period and baseline period. If a peak was absent, the power was considered "0".

2) Abundance of oscillations, defined as the percentage of trials within a condition in which a peak in the alpha or theta range is observed.

3) The aperiodic exponent.

4) The aperiodic offset.

Additionally, bandpower was collected as the average power within the frequency bands of interest. Resulting in five measurements per trial.

A baseline correction was performed by subtracting the baseline values of these parameters from the values of the retention period in a trial-by-trial fashion for all five outputs. Afterwards, each output was averaged per condition, participant, and across electrodes within each cluster.

2.3.4 Inclusion criteria for single-trial model fit

Model fit inspection was done by calculating the mean R^2 per condition and per participant. Trials with a model fit lower or higher than twice the standard deviation of the mean were removed from further analysis. Afterwards, participants were checked again for having enough trials per condition (minimum of 75 in Experiment 1, and minimum of 40 in Experiment 2) to remain included in this study. This resulted in excluding four participants in Experiment 1 and another four in Experiment 2 for the occipitoparietal analysis. No participants were excluded based on this criterion in either experiment for the frontal midline analysis.

2. 4 Behavioral analysis and correlation to EEG metrics

WM capacity was calculated in two ways. The first was based on the main task while EEG was recorded, by calculating the average number of items correctly remembered over all trials. The second method was based on the performance during a baseline WM task which followed the same procedure in both experiments (referred to as the Color Change Detection Task in Adam et al., 2018). This WM estimate was calculated per set size, and then averaged to get a single value representing WM capacity per participant, expressed as an estimate ("K") which is calculated with the following formula:

K = N x (H - FA)
N = set size
H = hit rate (proportion of correct trials)
FA = false alarm rate (proportion of incorrect no-change trials)

2.5 Statistical analysis

The dependent variables in both experiments were the oscillatory power relative to the aperiodic signal, oscillation abundance, aperiodic exponent, aperiodic offset, and bandpower

For the occipitoparietal region, separate two-factor repeated measures ANOVAs were applied on all dependent variables. The factors were set size in Experiment 1 (one, three, six) or performance in Experiment 2 (good, poor) and lateralization (ipsilateral, contralateral). In cases where the ANOVA was significant, pairwise t-tests with Bonferroni correction were applied as post-hoc tests to examine the differences between the levels within each factor. For the frontal midline region, separate repeated measures ANOVA were applied to test for significant differences on all dependent variables between set sizes (Experiment 1), and pairwise t-tests were applied similarly to test statistical significance of performance (Experiment 2). Additionally, paired t-tests were applied on each variable averaged over the conditions to test whether there was a significant difference between the retention and baseline period.

Shapiro-Wilk tests were used to test for normality, Levene's test for equal variance, and Mauchly's test were used to test for sphericity. If sphericity was violated, the Greenhouse-Geisser correction was applied for the factorial repeated measures ANOVAs. If one or more assumptions were violated, a Friedman test was used instead of a repeated measures ANOVA, or the Wilcoxon signed rank test was used instead of a pairwise t-test. Cohen's d was reported as effect size for t-tests, partial eta-squared for ANOVA tests, and the Common-Language Effect Size (CLES) for non-parametric tests.

For our exploratory analysis, we investigated correlations between WM capacity and aperiodic exponent or offset, Pearson correlations were calculated with a Bonferroni threshold correction.

2.6 Software

All data were processed using the Python programming language (version 3.7.1). Signal processing was done with the *neurodsp* module (version 2.1.0) (Cole et al., 2019), and power spectra were fitted with the *specparam* toolbox (version 1.0.0) (Donoghue, Haller, Peterson, et al., 2020). All statistics were performed in Pingouin (version 0.5.2) (Vallat, 2018), and plots were created using Matplotlib (version 3.0.2) (Hunter, 2007) and seaborn (version 0.9.0) (Waskom, 2021).

2.7 Data and code statement

Data used in this project is from Adam et al. (2018), and is available at OSF (https://osf.io/8xuk3/). The code for the analyses carried out in this paper are available at our GitHub page.

3. Results

3.1 Successful replication of the original paper's results

All findings from the original paper (Adam et al., 2018) were first successfully replicated before moving onto the spectral parameterization analysis. These results can be found on our GitHub repository. In short, an increase in WM load was associated with a bigger decrease in lateralized occipitoparietal alpha power, and when separated by trial accuracy, theta power was higher for good WM performance than poor.

3.2 Spectral parameterization: separating oscillatory from aperiodic activity

3.2.1. Participants

For this analysis, only participants exhibiting alpha oscillations over occipitoparietal electrodes or theta power over frontal midline electrodes were included. Furthermore, they needed to pass the minimum number of trial requirements as well. All 30 participants in Experiment 1, and the majority (37 out of 44) in Experiment 2 exhibited clear peaks in the alpha range according to the spectral parameterization criteria. After excluding participants who did not meet the minimum number of trials requirement, we ended with a sample size of 26 in Experiment 1, and 26 in Experiment 2. In contrast, only 12 out of 30 participants in Experiment 1, and 19 out of 44 in Experiment 2 met the criteria for exhibiting putative theta oscillations, identified as peaks in the theta range. The final sample size after excluding participants is 10 in Experiment 1, and 17 in Experiment 2 (**Table 1**).

To increase the sample size and therefore statistical power for the aperiodic analyses on frontal midline electrodes, we decided to include participants that did not exhibit putative theta oscillations. In Experiment 1, 15 from the 18 participants without oscillations satisfied the minimum trial count requirement and were included here, bringing the total to 25 participants. In Experiment 2, 17 from the 27 met these criteria in Experiment 2, bringing that total to 34.

3.2.2 Experiment 1: Frontal midline aperiodic-adjusted theta power and aperiodic activity

All variables violated sphericity. From the 12 participants with putative theta oscillations, 2 were rejected due to low trial count. For the remaining 10 participants included in this analysis concerning theta oscillations, aperiodic-adjusted theta power was not significantly different between set sizes ($W(2) = 0.07$, $p = 0.50$). Theta power over the three set sizes was significantly higher during the retention period compared to baseline ($t(9) = 2.72$, $p = 0.024$, Cohen's $d = 0.54$). Similar to the theta power results, theta abundance was not significantly different between set sizes ($W(2) = 0.01$, $p = 0.90$). In contrast to power, there was a significant decrease in abundance from baseline over all conditions ($W = 7$, $p = 0.037$, CLES $= 0.36$).

Frontal midline aperiodic exponent and offset were calculated for all participants included ($n = 25$), not just the participants that also had theta power. The frontal aperiodic exponent was not significantly different between set sizes ($W(2) = 0.04$, $p = 0.34$), but was significantly decreased from baseline over all conditions ($W = 66$, $p = 5.6*10^{-3}$, CLES $= 0.48$). A similar pattern was observed for the frontal midline offset; no significant differences between set sizes ($W(2) = 0.046$, $p = 0.30$), but aperiodic offset was significantly reduced from baseline over all conditions ($W = 0.046$, $p = 8.3*10^{-5}$, CLES $= 0.44$). Theta bandpower was not significantly different between set sizes ($W = 0.028$, $p = 0.48$), but was also significantly reduced during the retention period over all set sizes ($W = 89$, $p = 2.9*10^{-2}$, CLES $= 0.46$).

These results, leveraging the novel spectral parameterization method, suggest that theta oscillations are less frequently observed over trials in the retention period compared to baseline, but they demonstrate higher power (peak height) when present. Additionally, we found that the aperiodic exponent and offset reduced significantly during the WM retention period, but no differences due to WM load were observed in any of the frontal midline metrics for Experiment 1.

3.2.3 Experiment 2: Frontal midline aperiodic-adjusted theta power and aperiodic activity

Seventeen participants met all inclusion criteria for theta oscillation analyses. Aperiodic-adjusted theta power was not significantly different between poor and good performance ($t(16) = -1.59$, $p = 0.13$, Cohen's $d = -0.48$), nor was theta power different during the retention period from baseline ($t(16) = 2.05$, $p = 0.057$, Cohen's $d = 0.36$). Similarly, theta abundance was not significantly different between poor and good performance ($t(16) = 1.08$, $p = 0.30$, Cohen's $d = 0.41$), nor was it different from baseline to retention ($t(16) = -1.62$, $p = 0.12$, Cohen's $d = 0.23$).

The midline frontal aperiodic exponent and offset were calculated for all included participants ($n=34$), not just the participants that also had theta power. Neither were normally distributed; therefore the

non-parametric Wilcoxon signed-rank test was used to determine statistical significance. The exponent was not significantly different between performances (W = 280, p = 0.77, CLES = 0.54), but it was significantly decreased from baseline (t(32) = -2.37, p = 0.024, Cohen's d =0.14). Aperiodic offset was not significantly different between performances (W = 283, p = 0.81, CLES = 0.52), offset was significantly reduced from baseline (t(32) = -4.09, p = $2.7*10^{-4}$, Cohen's d = 0.27). Theta bandpower in showed no difference between performances (t(25) < 1.0), but was significantly reduced during the retention period from baseline (W = 135, p = $9.6*10^{-3}$, CLES = 0.45).

In contrast to Experiment 1, we found that theta abundance as identified via spectral parameterization did not differ by task-state (baseline vs. retention) nor by task performance. Similarly, to Experiment 1, task state (retention vs. baseline) induced a significant reduction in aperiodic exponent and offset. These results stand in contrast to the original paper that found higher theta activity in trials with good performance than poor performance, using the traditional filter-Hilbert analysis approach that mixes aperiodic and oscillatory activity. Thus, it comes as a surprise to not observe differences between performances for both aperiodic measures, nor for aperiodic-adjusted theta power.

3.2.4 Experiment 1: Occipitoparietal aperiodic-adjusted alpha power and aperiodic activity

Using a two-way repeated measures ANOVA, there was a main effect of set size on aperiodic-adjusted occipitoparietal alpha power (F(2,50) = 6.25, p = $3.8*10^{-3}$, $\eta_p^2 = 0.20$), but not for lateralization (F(1,25) = 1.17, p = 0.29, $\eta_p^2 = 0.045$). Alpha power in set size one was significantly higher than set size three (t(25) = 2.10, p = 0.046, Cohen's d = 0.39), and set size six (t(25) = 3.10, p = $4.7*10^{-3}$, Cohen's d = 0.64), but not different between set size three and six (t(25) = 1.59, p = 0.13, Cohen's d = 0.18). The interaction between set size and lateralization was not significant (F(2,50) = 2.95, p = 0.061, $\eta_p^2 = 0.11$). Alpha abundance was significantly different between set sizes (F(2,50) 3.59, p = 0.035, $\eta_p^2 = 0.13$), with the post-hoc only showing a significant increase from set size one to six (t(25) = -2.44, p = 0.022, Cohen's d = -0.40). Main effect of lateralization was not significant, nor in the interaction (F < 1.0).

There was a main effect of set size on occipitoparietal aperiodic exponent such that it decreased with increasing set size (F(2,50) = 5.99, p = $4.6*10^{-3}$, $\eta_p^2 = 0.19$). A post-hoc test shows that the difference is significant between set sizes one and six (t(25) = 3.08, p = $5.0*10^{-3}$, Cohen's d = 0.52), and between set sizes three and six (t(25) = 2.35, p = 0.027, Cohen's d = 0.26). No significant effect was found for lateralization, nor was there an interaction effect between lateralization and set size (F < 1.0). Furthermore, exponent was significantly decreased from baseline over all conditions (t(25) = -5.43, p = $1.2*10^{-5}$, Cohen's d =0.22). Occipitoparietal aperiodic offset was also significantly decreased with increasing set sizes (F(2,50) = 7.68, p = $1.2*10^{-3}$, $\eta_p^2 = 0.23$). A post-hoc pairwise t-test shows that this difference is between set sizes one and six (t(25) = 3.30, p = $2.9*10^{-3}$, Cohen's d = 0.64), and between set sizes three and six (t(25) = 3.01, p = $5.9*10^{-3}$, Cohen's d = 0.34). Furthermore, over all conditions the offset was significantly lower during the retention period compared to baseline (t(25) = -6.93, p = $2.9*10^{-7}$, Cohen's d = 0.32). Bandpower showed a main effect of set size (F(2,50) = 7.18, p = $1.8*10^{-3}$, $\eta_p^2 = 0.22$), but not for lateralization (F(1,25) < 1.0) or their interaction (F(2,50) = 2.98, p = 0.060, $\eta_p^2 = 0.11$). Post-hoc tests showed that all three set sizes were significantly different from each other. Set size one had the lowest bandpower, lower than set size three (t(25) = 2.15, p = $4.2*10^{-2}$, Cohen's d = 0.36), and set size six (t(25) = 2.95, p = $6.8*10^{-3}$, Cohen's d = 0.54), and set set size three was lower than set size six (t(25) = 3.74, p = $9.5*10^{-4}$, Cohen's d = 0.15).

In summary, we observed alpha peak height decrease with an increase in WM set size, but no differences between hemispheres. A lack of lateralization is in contrast with the original paper's findings. However, lateralization effects in alpha power in the literature are mixed (Adam et al., 2018, 2020; Medendorp et al., 2007; Sauseng et al., 2009; van der Werf et al., 2008; van Dijk et al., 2010). Aperiodic exponent and offset showed similar results, a decrease with an increase in WM set size, on top of an overall decrease during the retention period from baseline. These results show that aperiodic activity is involved in WM processes over occipitoparietal regions.

3.2.5 Experiment 2: Occipitoparietal aperiodic-adjusted alpha power and aperiodic activity

For aperiodic-adjusted alpha oscillations, we observed a significant main effect of performance (F(1,25) = 4.78, p = 0.038, $\eta_p^2 = 0.16$), in which power was lower in the good performance condition compared to the poor performance condition. But lateralization nor the interaction effect were significant (F < 1.0). Alpha abundance did not differ as a function of performance, lateralization, or their interaction (F < 1.0).

Occipitoparietal aperiodic exponent was not significantly different between performance, nor the interaction between performance and lateralization ($F < 1.0$), but it was for lateralization ($F(1,25) = 4.34$, $p = 0.048$, $\eta_p^2 = 0.15$) in which the contralateral hemisphere had a lower exponent than the ipsilateral hemisphere. The exponent was also significantly reduced during the retention period compared to baseline over all conditions ($t(25) = -4.99$, $p = 3.9*10^{-5}$, Cohen's $d = 0.24$). A similar pattern was observed for the offset; the contralateral hemisphere had a lower offset than the ipsilateral hemisphere ($F(1,25) = 6.08$, $p = 0.021$, η_p^2, $= 0.20$), and an overall reduction was found compared to baseline ($t(25) = -6.41$, $p = 1.0*10^{-6}$, Cohen's $d = 0.38$). Whereas alpha bandpower showed a main effect of set size in Experiment 1, no significant results were observed between good or poor performance in Experiment 2 ($F < 1.0$).

Alpha peak height was lower on good performance trials than poor, which is in line with our results for set sizes in Experiment 1. However, aperiodic exponent and offset did not show similar patterns as in Experiment 1, but it was lower over the ipsilateral hemisphere compared to the contralateral hemisphere, with this being the only time we observe lateralization effects. We did also observe overall reduced exponent and offset during the retention period from baseline. Hinting at a more WM task-general over task-specific involvement.

3.3 Correlations between working memory capacity and task-states

Given the importance that theta oscillations are said to play in WM, we next sought to examine whether there was a difference in WM capacity between participants for whom there was, versus was no, detectable theta oscillations with spectral parameterization. To test this, we looked at WM capacity in two ways, either as estimated from the performance on the WM task performed during the EEG experiment, or as measured from a baseline WM task collected prior to EEG recording. Notably, these two metrics of WM capacity were correlated within participants for both Experiment 1 ($r(25) = 0.56$, $p = 3.37 * 10^{-3}$) and Experiment 2 ($r(33) = 0.41$, $p = 0.018$).

We found no significant WM capacity differences between the groups of participants who exhibited or did not exhibit theta oscillations when measured from the main EEG task or from the baseline task, in either experiment ($p > 0.4$ in all instances). This indicates that WM capacity is not reliant on whether participants exhibited measurable theta oscillations.

In an additional exploratory analysis, we examined whether either measures of WM capacity correlated to aperiodic activity, exponent or offset from either frontal midline or occipitoparietal regions. We examined this using average pre-stimulus baseline aperiodic activity, during the retention period, and in the within-participant change from baseline to retention. This resulted in 24 correlations, with a Bonferroni corrected threshold of $p < 2.08*10^{-3}$. None of those correlations were significant under this criterion.

Finally, we noticed that there appeared to be a difference in the overall aperiodic-adjusted theta power between Experiments 1 and 2 (Fig. 3 A&G). Notably, in Experiment 1 set size could vary between one, three or six items, whereas in Experiment 2 the set size was constant at six items. To verify this visual observation, we performed t-test on relative theta power during the baseline, retention period, and their difference between Experiment 1 and 2. Relative aperiodic-adjusted theta power was significantly higher during Experiment 1 for both the baseline ($t(15.85) = 2.57$, $p = 0.020$, Cohen's $d = 1.09$) and retention periods ($t(12.49) = 2.56$, $p = 0.024$, Cohen's $d = 1.17$). However the difference in theta oscillatory power between baseline and retention was not significant ($t(14.83) = 1.36$, $p =0.19$, Cohen's $d = 0.59$).

These results indicate that aperiodic-adjusted theta power is overall higher during Experiment 1 with a variable WM set size, compared to Experiment 2 with a constant high WM set size, but the task-induced changes in relative theta power from baseline are similar. More information and figures can be found on our GitHub page.

4. Discussion

Many theories of human visual WM rely on theta and alpha oscillatory mechanisms for coordinating information flow between brain regions and as a neural code for memory (Lisman & Jensen, 2013; Palva & Palva, 2007). However, these theories are built on the flawed assumption that event-related changes in those frequency bands always capture oscillations. Here, we sought to explicitly examine whether and to what degree theta and alpha oscillatory activity is distinct from aperiodic activity in WM. Explicitly controlling for aperiodic activity, we find that fewer than half of participants (42%) had an identifiable theta peak in their power spectra. While not conclusive evidence for a lack of oscillations, this suggests that if

frontal midline theta oscillations are present in human EEG during WM, they are weak and/or rare. Therefore, it is likely that previous studies investigating the role of frontal midline theta in WM were more often than not largely capturing non-oscillatory aperiodic activity in the majority of participants, rather than true theta oscillations. If that is true, then it means that, while frontal midline theta may play a role in human WM, it is not a requirement for successful memory performance on any given trial.

Aperiodic-adjusted theta power increased during the retention period compared to baseline, but, consistent with previous analyses of these data, total theta bandpower actually decreased. This paradox, whereby theta simultaneously increases and decreases during WM retention, is mirrored by many mixed results regarding theta in human memory(Herweg et al., 2020; Pavlov & Kotchoubey, 2022). We believe this paradox can be explained by considering aperiodic activity, since we observed significant aperiodic decreases during WM retention, but surprisingly not between WM loads. If these aperiodic effects are ignored, they can mask and muddle the underlying oscillatory theta effects. **Thus, the mixed results regarding theta in human WM can partly be resolved by accounting for aperiodic dynamics.** The rarity of theta oscillations is an interesting contrast to the relative ubiquity of alpha oscillations. Even when accounting for aperiodic activity, we replicated the common finding that alpha power decreases with increasing WM load. A load-dependent decrease was also found for aperiodic activity. Thus, both ongoing alpha oscillations and aperiodic activity support visual attention and WM retention.

Importantly, we identified a task-general, and load-dependent decrease of aperiodic activity during WM retention. Aperiodic activity has potential links to underlying physiological mechanisms, offering a potential bridge across levels of analysis, relating spiking activity to LFP, and, by extension, scalp EEG. The aperiodic exponent at least partially reflects the balance of excitation and inhibition (E:I), as has been shown in a simple computational model involving GABA and AMPA currents (Gao et al., 2017), with pharmacological interventions (Colombo et al., 2019; Waschke et al., 2021), and using magnetic resonance spectroscopy imaging (McKeon et al., 2024). However, research using biophysical modeling challenges this perhaps overly simplistic hypothesis (Brake et al., 2024). Nevertheless, if aperiodic activity serves as an indicator of E:I, we can make insightful connections with computational models of WM that highlight the importance of a balanced E:I network to sustain activity for maintaining information (Lu et al., 2023; Wang, 1999). This sustained spiking activity is mostly asynchronous, and therefore has limited contribution to oscillating activity (Compte et al., 2000), making aperiodic activity a better candidate to study. Since these computational models are based on prefrontal cortex anatomy and dynamics, it is intriguing we only found load-dependent aperiodic decreases in occipitoparietal regions, but not over the frontal midline.

Thus, the task-general decreases in aperiodic activity observed in both frontal midline and occipitoparietal regions could indicate a shift in E:I balance that is supported by computational models of sustained activity during the maintenance period. The task-specific modulations in occipitoparietal regions support the sensory recruitment theory, in which sensory regions are actively involved in the maintenance of WM items (D'Esposito & Postle, 2015). In this case, occipitoparietal regions are involved in the maintenance of visual stimuli through asynchronous activity as well as oscillatory activity, whereas the frontal midline could be considered a top-down signal (Lara & Wallis, 2015).

While we found aperiodic flattening after stimulus onset on a visual WM task in frontal and anterior regions, others found steepening or mixed results (Akbarian et al., 2023; Frelih et al., 2024; Kałamała et al., 2024; Lendner et al., 2023; Virtue-Griffiths et al., 2022). Notably, some of these papers (Akbarian et al., 2023; Frelih et al., 2024) used the n-back task, which mixes motor preparation responses with WM maintenance activity (Pavlov & Kotchoubey, 2022). Mixed results were also observed on a visual continuous recall WM task; increased exponents over the frontal midline, and decreases over occipitoparietal regions, with an increase in exponent being associated with improved performance on a battery test (Virtue-Griffiths et al., 2022). Non-WM cognitive tasks suffer a similar fate; some find decreases in exponent after stimulus onset (Podvalny et al., 2015; Waschke et al., 2021), others find biphasic responses (Kałamała et al., 2024). These inconsistent results can be partly explained by choice

of task and whether fast motor responses are required, but also potentially driven by a lack of consistency in how aperiodic activity is measured and reported (Donoghue, 2024).

After correcting for aperiodic activity, we no longer observed a positive relationship between theta activity and WM load as in the original study. This lack of replication is likely driven by two factors. First, the large, event-related decrease in aperiodic activity is conflated with theta oscillations dynamics, which the filter-Hilbert approach cannot disentangle. Second, only 42% of participants had detectable theta oscillations according to spectral parameterization. Therefore, we could only analyze theta activity related to performance for a subset of participants. This finding is consistent with other research showing theta oscillations are surprisingly scarce within, and across, groups of participants (Bailey et al., 2020; Mitchell et al., 2008; Wilson et al., 2022). Notably, we did not find behavioral differences between participants exhibiting theta oscillations or not, and thus suggest the ability to detect theta oscillation at the scalp is due to anatomical (cortical folding, hippocampus orientation) or physiological, rather than behaviorally functional, differences.

In contrast to theta, almost all participants had detectable alpha oscillations (91%), which might contribute to the finding that alpha oscillations are less susceptible to masking by aperiodic dynamics than theta (Donoghue, Dominguez, et al., 2020). Correcting for aperiodic activity, we found an effect of relative alpha power due to WM load and performance. Furthermore, lateralized effects were only observed during the experiment using a high load only and separating trials based on WM accuracy, in which relative alpha power was more suppressed on the contralateral visual cortex of the attended hemifield. This is not a surprising finding, since the literature on lateralization effects are inconsistent (Adam et al., 2018, 2020; Fukuda et al., 2016; Sauseng et al., 2009). In summary, alpha oscillations in these datasets were involved in both visual WM and attention mechanisms (D'Esposito & Postle, 2015; Gevins & Smith, 2000; Halgren et al., 2002; Pavlov & Kotchoubey, 2022).

Though our results show aperiodic activity is involved in visual WM, there are methodological limitations to be addressed. First, performing spectral parameterization on task-based data means that we have shorter time windows than resting-state paradigms (Colombo et al., 2019; Helson et al., 2023; McKeon et al., 2024; Smith, Kosik, van Engen, et al., 2023; Waschke et al., 2021), resulting in noisy single trial power spectra. Although still feasible (Frelih et al., 2024; Höhn et al., 2024; Kałamała et al., 2024; Podvalny et al., 2015; Virtue-Griffiths et al., 2022; Waschke et al., 2021), we minimized this noise by rejecting trials based on model fits that were too low (indicating a bad fit), or too high (indicating overfitting noise), while still averaging the model output over a sufficient number of trials. Another issue became apparent while visually examining power spectra to determine whether participants exhibited oscillatory activity within the theta or alpha band. These canonical frequency bands are defined adjacent to one another, and some participants exhibited easily identifiable peaks in both bands, some only in one band, and others in neither. However, there were edge cases in which a lower center frequency alpha peak bled into the theta range, making them difficult to distinguish and to determine whether a peak should be considered alpha, or theta based on *a priori* frequency bands. This is already a concern for bandpass filters in which neighboring band activity infiltrates the band of interest (Pavlov & Kotchoubey, 2022).

Here, we have provided correlational evidence that aperiodic activity is involved in human visual WM and shown that it can mask frontal midline theta oscillatory dynamics. One way to causally disentangle the role of oscillatory versus aperiodic dynamics in human WM would be to leverage non-invasive neurostimulation. Neurostimulation is commonly used to study the causal role of oscillations, via transcranial Alternating Current Stimulation (tACS) (Grover et al., 2023). Because aperiodic activity consists of arrhythmic unstructured fluctuations, transcranial Random Noise Stimulation (tRNS) - where a white noise spectrum electrical current is introduced into the brain - is a better candidate to target endogenous aperiodic activity, thought white noise is quite different from endogenous aperiodic activity. It has been shown that tRNS flattens the spectrum (van Bueren et al., 2023), thereby effectively showing that aperiodic activity can be targeted with non-invasive electrical stimulation. Thus, it may be possible to

test the causal role of aperiodic activity in human visual WM using aperiodic stimulation that more closely mimics endogenous aperiodic activity.

While we did not observe load-dependent aperiodic changes over the frontal midline, we did reveal the possibility that previous frontal midline theta results that do not correct for aperiodic activity likely do not reflect theta oscillations. It will be interesting to investigate if our results based on extracranial EEG translate to intracranial EEG and animal models of WM, and if our results are driven by the imprecision of EEG to detect frontal midline theta oscillations. While our results do not invalidate previous research into extracranial theta oscillations in relation to WM, they challenge popular and widely held beliefs regarding the mechanistic role for theta oscillations to group or segregate channels of information (Lisman & Jensen, 2013). After all, if people can still reliably perform WM tasks in the absence of detectable theta oscillations, then either our detection ability is severely flawed, or our theories are incomplete (Van Bree et al., 2024).

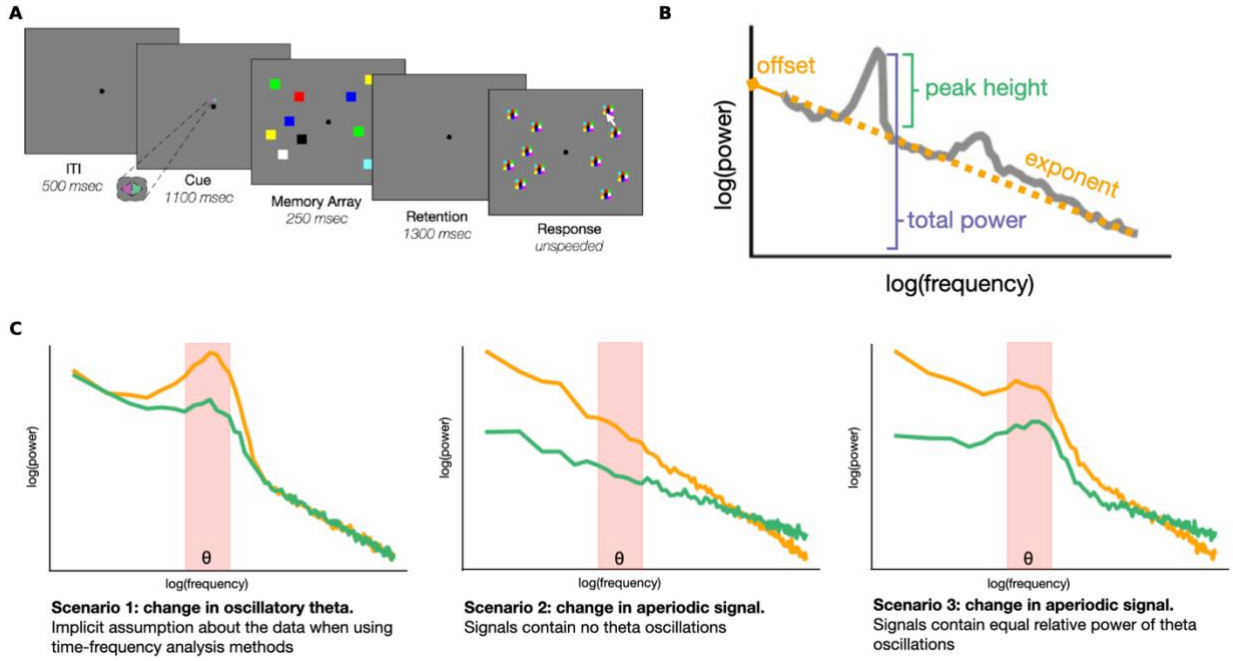

Figure 1: Overview of experiment, analysis, and hypotheses*. A) Visual description of the whole-report visual working memory task (adapted from Adam et al., 2018). A cue indicated whether participants were required to attend to the left or right side of the screen. Both sides contained the same number of colored squares, but in different locations. In experiment 1, set size was manipulated to consist of one, three or six items on each side. In experiment 2, the set size was kept constant at six items. After a 1300 ms retention period, participants were prompted to indicate the color of each item of the attended side. There were nine discrete colors to choose from. B) Spectral parameterization method. From a power spectrum, the aperiodic components, the exponent and offset, were quantified separately from the periodic components, relative power. Total power was captured as bandpower. C) Three scenarios illustrating how task-induced changes in the power spectrum appear as theta bandpower changes. The theta frequency range (4-7 Hz) is highlighted in red. Scenario 1 (left) shows the assumed model whereby task-related changes in theta band activity are driven by changes in narrowband, oscillatory theta activity manifesting above a stable aperiodic signal. Scenario 2 (middle) and 3 (right) describe situations in which a reduction in total theta power on the task (green line) from baseline (orange line) is observed, all driven by changes in aperiodic dynamics whether or not detectable theta oscillations are present.*

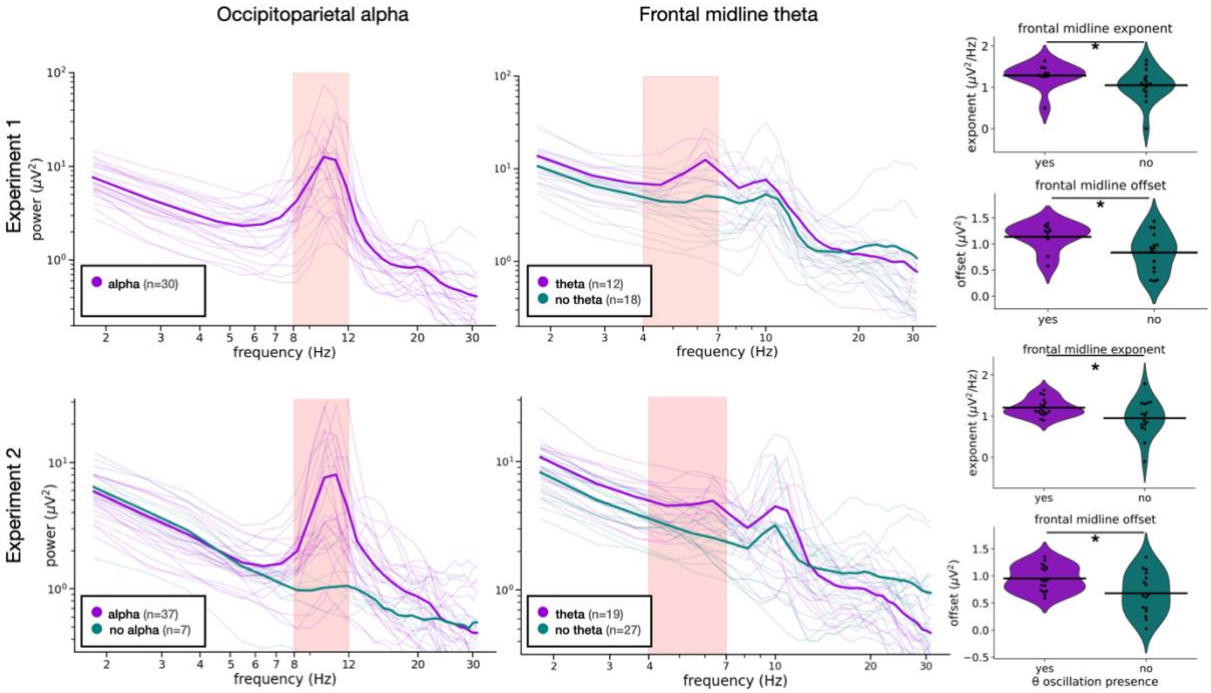

Figure 2: Grouping participants based on the presence of oscillatory peaks. *Here we show for both experiments (rows), and oscillatory bands (columns) the average (thick lines), and individual participant PSDs (thin lines) averaged over all trials for those who did exhibit oscillatory power (magenta), and those who did not (teal). For theta, we also observe group differences in both aperiodic exponent and offset, in which participants without theta oscillations typically have flatter spectra. These results apply to both experiments. * = p < 0.05*

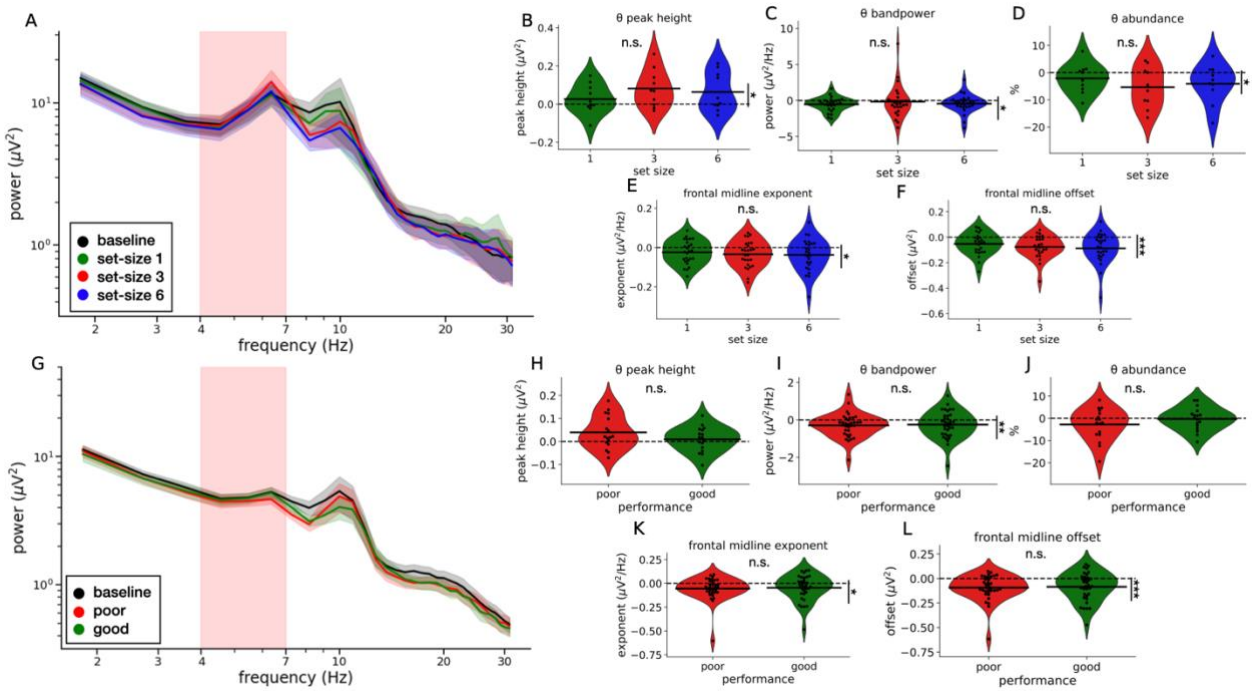

Figure 3: Frontal midline aperiodic activity decreases during the retention period from baseline, whereas theta oscillations increase in power. *A-F) Experiment 1 results. A) Shows the power spectra from baseline (black), and the three different set sizes. B) Theta peak height increases from baseline, whereas abundance (D) and bandpower (C) decreases. Aperiodic exponent (E) and offset (F) show no significant differences between set sizes, but are significantly decreased from baseline. G-L) Experiment 2 results. F) Shows the power spectra for the baseline (black), and poor (red) versus good (green) WM performance. No significant differences were observed in theta peak height (H), nor in abundance (J), whereas both bandpower (I), aperiodic exponent (K), and offset (L) decreased from baseline. * = p < 0.05, ** = p < 0.005, ***= p < 0.001, n.s. = not significant.*

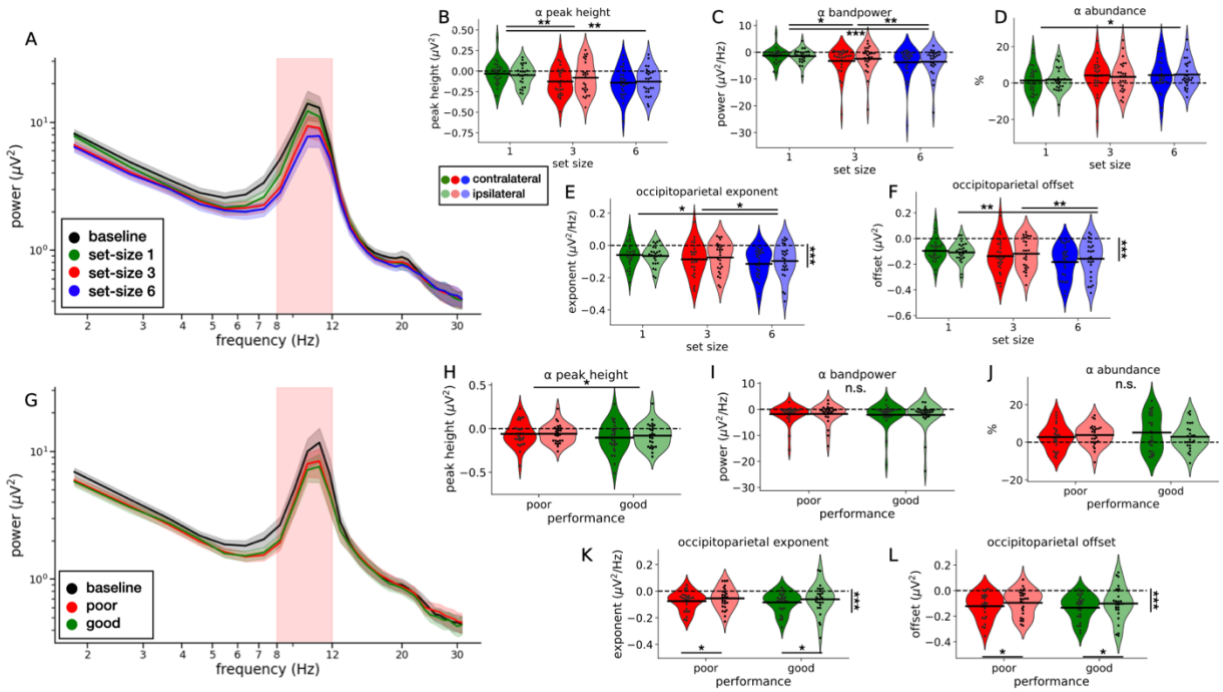

Figure 4: Occipitoparietal aperiodic activity decreases with increase in load, but not performance, whereas alpha oscillatory power follows classic findings. *A-F) Experiment 1 results. A) Shows the power spectra from baseline (black), and three set sizes. B) Occipitoparietal alpha peak height shows a significant decrease with an increase in WM load, but no lateralized effect is observed. Similar patterns are observed for total alpha bandpower (C), whereas abundance increases with set size (D). Aperiodic exponent (E) shows no lateralized effect, but there was a decrease with an increase in WM load. Similar patterns were observed for the aperiodic offset (F). G-L) Experiment 2 results. F) Shows the power spectra for the baseline (black), and poor (red) versus good (green) WM performance. A decrease in alpha peak height was observed for the good condition compared to the poor condition, but again no lateralization effect was found (H). Bandpower and (I) abundance (J) did not show any significant differences. The aperiodic exponent (K) and offset (L) were both significantly reduced from baseline, and a lateralization effect was observed, in which activity in the contralateral hemisphere was more suppressed than the ipsilateral hemisphere. * = p < 0.05, ** = p < 0.005, ***= p < 0.001, n.s. = not significant.*

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