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Theta and Alpha Oscillations Reflect Distinct Control and Stabilization Processes Across Working Memory

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What are the main findings?

- During the retrieval, where the participants responded to the probe, theta power was higher than in earlier working memory stages.
- Upper alpha power was associated with increased probability of correct responses, highlighting the role of specific oscillatory activity in performance.

What are the implications of the main findings?

- Theta oscillations may index the coordination of processes involved in task responses, such as accessing stored information and decision-making.
- Upper alpha activity may support performance in demanding cognitive tasks.

Abstract

Background/Objectives: The oscillatory dynamics underlying stage-specific processing in working memory (WM) remain incompletely characterized, particularly under varying memory loads. We examined load-dependent modulation of theta (4-7 Hz), lower alpha (8-10 Hz), and upper alpha (11-13 Hz) absolute power during encoding, maintenance, and retrieval using quantitative EEG in a modified Sternberg task that temporally dissociates these stages. **Methods:** Forty-five healthy young adults performed trials with memory sets of three, five, or six uppercase consonants followed by a lowercase probe. EEG data were analyzed using cluster-based permutation testing, and brain-behavior relationships were assessed using regression models. **Results:** Fronto-central theta power increased with memory load and was significantly higher during retrieval than during encoding or maintenance. Greater theta power during retrieval predicted faster reaction times in the three-letter condition. Alpha oscillations showed robust stage effects. Lower alpha power was higher during maintenance than retrieval across loads and exhibited a load effect during maintenance (three > six letters) in occipital regions. Upper alpha power was consistently maximal during maintenance across all loads, involving bilateral fronto-central, parietal, and occipital regions. Critically, under moderate load (five letters), higher upper alpha power predicted a greater probability of correct responses across task stages. **Conclusion:** These findings demonstrate a functional dissociation between oscillatory bands across temporally separated WM stages: theta activity was retrieval-dominant and associated with response speed, whereas alpha, particularly upper alpha, was maintenance-dominant and supported accuracy under increased mnemonic demand.

Keywords: working memory; Sternberg task; EEG; theta; alpha

1. Introduction

Working Memory (WM) is among the most studied cognitive constructs. It refers to the cognitive system that temporarily stores and manipulates information necessary for complex tasks such as reasoning, problem-solving, and language comprehension [1].

The processing stages of working memory can be broadly categorized into encoding, maintenance/manipulation, and retrieval, each of which is associated with distinct cognitive processes [2]. Each stage requires coordination of neural circuits across multiple brain regions, particularly those associated with the prefrontal cortex, which is crucial for regulating attention, decision-making, and memory [3,4]. Attention is vital for selecting relevant information and inhibiting distractions, but it is limited by processing resources. Thus, cognitive load can significantly impact performance across all stages of working memory processing [5]. Cognitive load theory [6] emphasizes that there are limits to the amount of information working memory can handle simultaneously, and exceeding these limits can result in cognitive overload, reducing performance. Load can be influenced by the complexity of the information and the individual's cognitive capacity. A higher WM load has been shown to impair the ability to perform tasks efficiently, such as reasoning or problem-solving [7]. While it has been proposed that a higher WM load increases distractor interference [8], which may hinder further performance, it has also been argued that both perceptual and WM loads decrease distractor processing as cognitive demands rise [9]. These effects might depend on the tasks used and the type of cognitive load [10].

Although several neuroimaging studies have identified distinct neural substrates of WM processing, such as the dorsolateral prefrontal and posterior sensory cortices [1,11], our understanding of their temporal functional dynamics is limited. Electrophysiological studies can capture time-sequential processes and have also been shown to be sensitive to memory load [12].

Quantitative EEG (qEEG) measures, in particular, have been widely used in this context to understand memory processes. Data from theta and alpha frequency bands have been closely associated with cognitive processes such as attention, long-term memory, and working memory [13-15]. The different stages of working memory likely reflect a changing configuration of overlapping processes (e.g., attention, manipulation, decision-making), with task design biasing the relative dominance of these operations over time. Therefore, the observed activity of theta and alpha, rather than being strictly stage-specific neural signatures, probably indicates stage-weighted oscillatory dynamics. Theta power in the frontal region has been observed to increase at stimulus presentation, suggesting that this activity relates to initial encoding processes that involve attention allocation to a task, independent of modality [16]. Additionally, theta oscillations have been linked to visual information processing, as they increase in occipital areas immediately after stimulus presentation, followed by decreases in power and increases in frontal regions during an n-back task [17]. However, this type of task involves multiple processes, such as encoding, updating, maintaining, and matching of information that take place in a parallel manner and involve numerous brain regions [18,19], making it difficult to study each of the processes that primarily relate to the stages of WM. Likewise, there is evidence of higher theta power in the right frontal areas during encoding, compared with activity during information retrieval in a visuospatial virtual reality task [20].

Theta-band activity has also been linked to maintaining information with increasing absolute power at higher memory loads. This finding has been reported in different studies, and it is most commonly associated with an increase in power in frontal and prefrontal areas [21,22], while there is evidence of sustained theta activity in all stages of working memory, from encoding to retrieval where there is a spread of activity from frontal to posterior areas [16]. However, in intracranial recordings from epilepsy patients, it was found that theta frequency power increases during maintenance in the hippocampus and dorsal anterior cingulate cortex (dACC) and decreases in the dorsolateral prefrontal cortex (DLPFC) proportional to memory load, thus suggesting that theta band power participates in different cognitive functions, playing a relevant role in the maintenance of information by decreasing theta power in DLPFC [23].

Additionally, alpha power decreases with increased task demands, particularly in frontal regions during maintenance and retrieval [17]. However, a decrease in alpha power in parietal areas has been associated with increased arousal, resource allocation, and workload [24,22], processes that occur continuously from encoding to retrieval across different task conditions. For instance, alpha power has been observed to increase in prefrontal areas during visuospatial manipulation compared with maintaining information in working memory [25]. Empirical data suggest that the increase in frontal alpha power during maintenance, compared to encoding and retrieval, where alpha power decreases, contributes to the inhibition of irrelevant or distracting information, implying that alpha may actively participate in attentional processes [26], probably reflecting top-down attentional control of relevant information. In this regard, frontal alpha oscillations exert top-down control of perceptual gains, while parietal alpha oscillations relate to intersensory re-orienting [27].

Several studies suggest that the alpha band is not functionally homogeneous. It can be subdivided into lower and upper alpha components, which appear to support partially distinct cognitive processes. Lower alpha (approximately 8-10 Hz) has been mainly associated with attentional demands and general task engagement. Upper alpha (approximately 10-13 Hz) has been more closely linked to semantic processing, working memory load, and top-down control mechanisms [14,28,29]. In working memory paradigms, upper alpha activity increases with memory load, reflecting active maintenance and manipulation of information. In contrast, lower alpha activity may reflect attentional gating and sensory disengagement [30,12]. Based on these findings, the present study analyzed lower and upper alpha to explore whether distinct sub-bands show differential modulation across working memory stages and load conditions.

Separating the different cognitive processes that occur during WM is challenging, if not impossible, due to their temporal overlap, the involvement of selective attention, and top-down control across all processing stages [31-33]. Despite extensive research on theta and alpha oscillations during working memory tasks, several important issues remain unresolved. First, many previous EEG studies have relied on paradigms such as the n-back task, in which encoding, updating, maintenance, and retrieval processes occur in parallel, limiting the ability to study stage-weighted neural dynamics. Second, although both theta and alpha oscillations have been associated with working memory load, findings remain inconsistent regarding their modulation across distinct processing stages and cortical regions. Third, few studies have simultaneously examined the interaction between memory load, processing stage, and regional distribution of oscillatory activity using a paradigm that allows clear temporal separation of encoding, maintenance, and retrieval.

The present study addresses these gaps by using a modified Sternberg item-recognition task that permits the sequential dissociation of working memory stages, combined with quantitative EEG measures of absolute theta and alpha power. By manipulating memory load and examining oscillatory activity across fronto-central and parieto-occipital regions, we aim to characterize the stage-specific and load-dependent dynamics of these frequency bands. This approach allows for a more precise evaluation of how theta and alpha oscillations contribute differently to encoding, maintenance, and retrieval processes.

We hypothesized that theta oscillations would show load-dependent increases and stage-specific modulation reflecting executive engagement. Given the proposed inhibitory role of alpha oscillations, we expected stage-dependent changes, particularly during maintenance, as well as possible load-related effects that vary across cortical regions. By clarifying the temporal and regional specificity of these oscillatory patterns, this study seeks to contribute to the current neurophysiological models of working memory and to the interpretation of qEEG markers in both experimental and clinical contexts.

2. Materials and Methods

2.1. Participants

Forty-five healthy, right-handed university individuals (23 female, 22 male) between 20 and 30 years old (*M* = 23, *SD* = 2) with typical estimated IQs (WAIS-IV abbreviated version, *M* = 107, *SD* = 10) were recruited through personal invitation and social networks. All of them had an undergraduate degree or were studying at the time of the examination, with at least 1 year in their college program (years of schooling: *M* = 15, *SD* = 1). We estimated each individual's working memory index using the WAIS-IV's arithmetic and digit span tests (*M* = 99, *SD* = 9). An interview, brief clinical history, and the WAIS-IV tests were applied to the participants before the EEG recording and the experimental task. The participants were compensated with a brief report of their estimated IQ.

None of the participants had antecedent clinical neurodevelopmental, neurological, or psychiatric conditions, nor did they report memory or attention-specific complaints during the interview. Ethical approval was received before testing from the Neuroscience Institute's Ethics Committee (ET022023-359). All participants voluntarily agreed to participate and provided written informed consent.

2.2. Sternberg Item Recognition Task

The experimental task was a modified Sternberg task with three levels of memory load. The stimuli consisted of strings of three (low memory load), five, and six capital consonant letters (higher memory load). All the letters constituting one string were presented in white on a black background, separated by a space from one another. Each string appeared at the center of a screen for 3000 ms (a period we called the *encoding stage*, although this process might occur during the first lapse of this time [4]) and was followed by a period of 3000 ms with only a central fixation point (maintenance stage). Later, the maintenance period was followed by the appearance of a centrally located white lowercase letter lasting 2000 ms (retrieval stage) in which the individual had to respond by pressing, as fast as possible, a green button if the letter corresponded to its capital one in the preceding string or a red button if it did not. A 500 ms inter-trial interval followed this period, and the subsequent trial began immediately afterward. The position of the target digit within the memorized sequence (e.g., first digit of the sequence, second digit of the sequence, etc.) was completely randomized. The schematic experimental flow is shown in Figure 1.

A total of 120 trials (40 for each memory load condition) were administered. The stimuli were presented in 4 blocks of 30 pseudo-randomized trials (10 for each memory load level). All trials within a block were presented automatically, one after the other, until the end of the block. The participants had a brief break between blocks, starting the next block at their own pace. A direct visual-matching strategy was prevented using lowercase letters as probes.

Before the experimental session, participants had a practice block of seven trials, consisting of numbers for the strings and probes, while maintaining the same temporal parameters.

We used Compumedics Neuroscan Stim2 software to program and run the task, and a Cedrus' StimTracker Duo and RB-740 response pad to record behavioral responses. Participants were seated in a dimly lit room, ~60 cm distance from a 27-inch AOC 27G2 monitor with a 144 Hz refresh rate and 1920x1080 screen resolution. The visual angle was 1.81°.

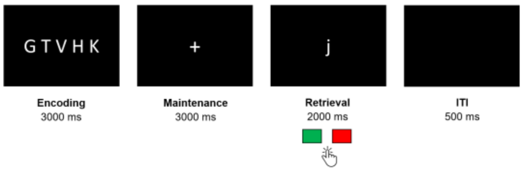

Figure 1. One trial of the modified Sternberg item recognition paradigm. The participants had to press the green button if the letter presented during retrieval was within the string of letters presented at encoding, otherwise they had to press the red button. ITI "inter-trial-interval".

2.3. EEG Recording and Processing

EEG data were acquired using a Compumedics Neuroscan Grael 4K EEG amplifier, a 32-channel Quick-Cap Neo Net, and Curry 9 X software. EEG was recorded from 28 channels according to the 10/20 system (Fp1, Fp2, F7, F3, Fz, F4, F8, FC3, FCz, FC4, T7, C3, Cz, C4, T8, CP3, CPz, CP4, P7, P3, Pz, P4, P8, O1, Oz, O2, M1, M2), with four additional periocular bipolar channels to record blinks and eye movements. The sampling rate was 2048 Hz, and interelectrode impedance was below 5 kΩ.

The continuous EEG data were first preprocessed and segmented into non-overlapping epochs using EEGLAB [34] functions and custom MATLAB scripts. The data were downsampled to 500 Hz and filtered with a 0.05 Hz high-pass finite-impulse response (FIR) filter. Line noise was removed using the CleanLine plugin, and the Clean Rawdata plugin was also applied to identify flatline and noisy channels. A spherical spline method was used to interpolate noisy channels. Afterward, the recording was re-referenced to the common average reference. To optimize artifact separation, independent component analysis (ICA) was estimated on a copy of the data that had been high-pass filtered at 1 Hz, which reduces the influence of slow drifts and improves component decomposition [35]. The resulting ICA weights were then applied to the minimally filtered data (0.05 Hz high-pass) to preserve low-frequency neural activity for subsequent analysis. Component rejection (primarily eye artifacts) was performed manually based on its spectral and temporal characteristics.

After preprocessing, the first second of each processing stage was selected for analysis. For each subject, we kept the same number of epochs across conditions (memory load and processing stage) with a group mean of 23 epochs ($SD = 3$). The subject with the least number had 20 epochs, and the subject with the maximum had 32 epochs (20 and 8 trials rejected, respectively). This was achieved by visually inspecting each trial and rejecting those that were incorrect or contaminated with eye artifacts or muscle activity that could not be removed with ICA. The power spectrum was calculated using Fast Fourier Transform (FFT) with a Hamming window of 500 data points and a 250-point overlap. Finally, we analyzed the mean absolute power in each frequency band (theta: 4-7 Hz, lower alpha: 8-10 Hz, upper alpha: 11-13 Hz) for each processing stage and memory load condition. Absolute power was also computed for the inter-trial interval and used as a baseline reference. Task-related power was normalized relative to this baseline using a decibel (dB) transformation.

2.4. Analysis

We used a repeated measures analysis of variance (ANOVA) to identify differences in accuracy (percentage of correct responses) and reaction time (milliseconds) between the different levels of memory load. The Greenhouse-Geisser correction was applied when necessary, and a Bonferroni correction was used for multiple comparisons.

Electrophysiological data were analyzed using cluster-based permutation testing for each contrast, an approach that leverages the spatial dependency structure of EEG signals. Rather than evaluating each electrode independently, this method tests whether there are spatially contiguous clusters of electrodes showing consistent effects that are unlikely to arise by chance. At each iteration, a t-test was computed at every electrode, and values exceeding the critical threshold of $t(44) = 2.01$ (corresponding to $p < .05$, uncorrected) were retained. Spatially adjacent significant electrodes were grouped into clusters, and the t-values within each cluster were summed to obtain the cluster-level statistic (t-sum). The maximum cluster-level statistic from each iteration was used to construct the null distribution. This procedure was repeated 5000 times. Clusters were defined based on a maximum inter-electrode distance of 40 mm.

To control for multiple comparisons across contrasts, a global null distribution of maximum cluster-level statistics was generated by selecting the highest cluster-level value across all contrasts at each permutation. Cluster-level statistics derived from the observed data were then compared against this global null distribution to determine statistical significance. This procedure was conducted separately for each frequency band. For significant clusters, effect sizes were estimated using Cohen's d, calculated using the mean absolute power of the elements comprising a cluster.

To examine the relationship between absolute power magnitude and behavioral performance, generalized linear models were fitted. Accuracy was analyzed using a binomial generalized linear model with absolute power as the predictor and number of correct responses as the dependent variable. Reaction time was analyzed using linear regression models. Each frequency band was tested separately. Because analyses were conducted for each electrode and condition, false discovery rate (FDR) correction was applied to control for multiple comparisons. Only electrodes belonging to significant clusters were included in these regression analyses.

3. Results

3.1. Behavioral Data

The ANOVA showed a significant effect of memory load on accuracy ($F(2, 88) = 60.7$, $p < .001$, $\eta^2 = .58$), with accuracy decreasing as memory load increased. The percentage of correct responses was higher at the three-letter memory load ($M = 95.44$, $SD = 3.93$) than at the five letter ($M = 87.22$, $SD =$

7.69, $p < .001$) or six letter ($M = 85$, $SD = 6.87$, $p < .001$) memory loads. There was no significant difference between five and six letters.

The memory load also had a significant effect on reaction time, which increased with the increase in memory load ($F(1.72, 75.76) = 61.8$, $p < .001$, $\eta^2 = .58$). Reaction time was higher in the memory load of five letters ($M = 921.64$, $SD = 115.68$, $p < .001$), and six letters ($M = 926.26$, $SD = 148.68$, $p < .001$) compared to three letters ($M = 816.58$, $SD = 111.03$). There was no significant difference in reaction time between five and six letters.

3.2. Electrophysiological Data

3.2.1. Theta

Processing-stage effects: Theta power was significantly higher during retrieval than during encoding across memory loads. At three letters, this effect involved bilateral and midline fronto-central-parietal regions ($p < .01$). At five letters, the effect was restricted to left and midline fronto-central-parietal regions ($p < .05$). At six letters, it was limited to left fronto-central regions ($p < .05$).

Additionally, at three letters, retrieval elicited higher theta power than maintenance in left and midline regions ($p < .01$). At six letters, maintenance showed higher theta power than encoding in right and midline regions ($p < .05$). Figure 2 shows the absolute power of the theta frequency band per condition and working memory processing stage, while Table 1 summarizes the results.

Memory load effects: During maintenance, theta power was higher at six letters compared to three letters in a midline fronto-central cluster ($p = .035$). In contrast, during retrieval, theta power was higher at three letters compared to six letters in right fronto-central regions ($p = .049$).

Brain-behavior association: In the three-letter condition, increased theta power at FCz during retrieval predicted faster responses, $b = -43.00$, $SE = 10.78$, $t(43) = -3.99$, $p < .001$, $r^2 = .27$. No associations with accuracy were observed.

Overall, theta activity was primarily enhanced during retrieval and was behaviorally relevant under low memory load.

Table 1. Summary of the statistical results for the effects of processing stage and memory load on the theta band absolute power.

Comparison	Memory load	Direction of effect	Main topography	*t*-sum	*p*	*d*
Encoding vs. Retrieval	3 letters	Encoding < Retrieval	Bilateral and midline fronto-central-parietal	-21.32 - -14.54	< .001 - .008	.55 - .75
	5 letters		Left and midline fronto-central-parietal	-17.24 - -12.31	.001 - .036	.53 - .71
	6 letters		Left fronto-central	-14.02	.013	.66
Maintenance vs. Retrieval	3 letters	Maintenance < Retrieval	Left and midline fronto-central-parietal	-22.84 - -16.51	< .001 - .002	.67 - .69
Encoding vs. Maintenance	6 letters	Encoding < Maintenance	Right and midline fronto-central-parietal	-14.49 - -13.09	.009 - .024	.58 - .60
Memory load effect (Maintenance)	3 < 6 letters	Higher theta at 6 letters	Midline fronto-central	-12.38	.035	.56
Memory load effect (Retrieval)	3 > 6 letters	Higher theta at 3 letters	Right fronto-central	11.36	.049	.38
Brain-behavior association	3 letters (Retrieval)	Higher theta - lower reaction time	FCz (fronto-central)		< .001	$r^2 = .27$

Topography summarizes significant electrode clusters. The values are the minimum and maximum values of each statistic (*t-sum*, *p*, and Cohen's *d*). In the brain-behavior association, regression results indicated that higher theta power was associated with faster reaction times.

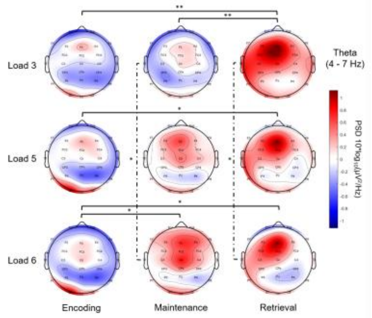

Figure 2. Absolute power of the theta frequency band in each condition and working memory processing stage averaged across participants. The specific cluster statistic values and *p* values are in table 1. * $p < .05$; ** $p < .01$; *** $p < .001$.

3.2.2. Lower Alpha

Processing-stage effects: Stage-related differences varied by memory load. At three letters, maintenance elicited higher lower-alpha power than encoding in midline fronto-central-parietal regions ($p = .006$). Maintenance also exceeded retrieval in bilateral fronto-central and parietal regions ($p \leq .001$).

At five and six letters encoding elicited higher lower-alpha power than retrieval (left hemisphere at five letters, $p < .001$; bilateral at six letters; all $p < .05$). Also, at both memory load levels, maintenance exceeded retrieval in bilateral and midline fronto-central-parietal regions (all $p \leq .008$).

Memory load effects: During maintenance, lower alpha power was higher at three letters than at six letters in occipital regions ($p = .022$). No significant associations were found between lower alpha power and behavioral performance.

In summary, lower alpha power was predominantly elevated during maintenance, particularly under lower load, whereas encoding-related increases emerged at higher loads. Figure 3 shows the absolute power of the lower alpha frequency band for each condition and working memory processing stage, while Table 2 summarizes the results.

Table 2. Summary of the statistical results for the effects of processing stage and memory load on the lower alpha band absolute power.

Comparison	Memory load	Direction of effect	Main topography	*t*-sum	*p*	*d*
Encoding vs. Maintenance	3 letters	Encoding < Maintenance	Midline fronto-central-parietal	-16.7	.006	.54
Encoding vs. Retrieval	5 letters	Encoding > Retrieval	Left fronto-central-parietal	23.2	< .001	.85
	6 letters		Bilateral fronto-central-parietal	14.7 - 20.4	.03 - < .001	.59 - .76
Maintenance vs. Retrieval	3 letters	Maintenance > Retrieval	Bilateral and midline fronto-central-parietal	19.1 - 27.8	≤ .001	.65 - .95
	5 letters			16.5 - 20.6	.01	.47 - .67
	6 letters			24.3 - 27.1	< .001	.56 - .72
Memory load effect (Maintenance)	3 > 6 letters	Higher lower alpha at 3 letters	Occipital	15.0	.02	.63

Topography summarizes significant electrode clusters. The values are the minimum and maximum values of each statistic (*t-sum*, *p*, and Cohen's *d*).

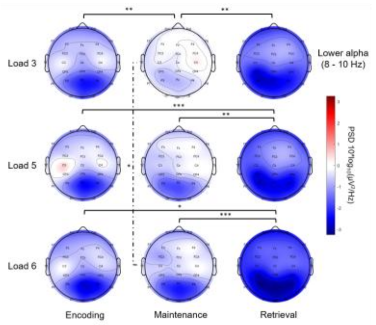

Figure 3. The absolute power of the lower alpha frequency band in each condition and working memory processing stage averaged across participants. The specific cluster statistic values and *p* values are in table 2. * *p* < .05; ** *p* < .01; *** *p* < .001.

3.2.3. Upper Alpha

Upper alpha showed the most consistent and robust effects across conditions.

Processing-stage effects: Across all memory loads, maintenance elicited higher upper alpha power than encoding in midline and right fronto-central-parietal regions, as well as occipital areas (all $p \leq .005$). Also, maintenance exceeded retrieval in bilateral fronto-central-parietal and occipital regions (all $p < .001$), with large effect sizes (many $d > 1$). Finally, encoding elicited higher upper alpha power than retrieval in left fronto-central-parietal regions across all loads (all $p < .001$). Thus, upper alpha activity was maximal during maintenance, regardless of memory load.

Memory load effects: During retrieval, upper alpha power was lower at six letters compared to three letters in midline fronto-central-parietal regions ($p = .006$).

Brain-behavior associations: In the five-letter condition, higher upper alpha power was associated with a greater probability of correct responses across encoding, maintenance, and retrieval stages in left fronto-central and occipital regions (FDR-corrected $p \leq .044$). Odds ratios ranged from 1.08 to 1.18, indicating that increased upper alpha power significantly improved the likelihood of correct responses. No associations were observed between upper alpha power and reaction time. Figure 4 shows the absolute power in the upper alpha frequency band for each condition and working memory processing stage, while Table 3 summarizes statistical analysis results.

Table 3. Summary of the statistical results for the effects of processing stage and memory load on the upper alpha band absolute power.

Comparison	Memory load	Direction of effect	Main topography	*t*-sum	*p*	*d*
Encoding vs. Maintenance	3 letters	Encoding < Maintenance	Midline fronto-central-parietal; occipital	-23.31 - -23.28	< .001	.82 - 1.23
	5 letters		Midline and right fronto-central-parietal; occipital	-23.31 - -20.59	< .001	.65 - 1.11
	6 letters			-18.94 - -17.45	.002–.005	.60 - .98
Maintenance vs. Retrieval	3 letters	Maintenance > Retrieval	Bilateral and midline fronto-central-parietal; occipital	22.42 - 41.23	< .001	.95 - 1.54
	5 letters			22.41 - 43.96	< .001	.94 - 1.52
	6 letters			24.77 - 48.19	< .001	.92 - 1.38
Encoding vs. Retrieval	3 letters	Encoding > Retrieval	Left fronto-central-parietal	26.06	< .001	1.39
	5 letters			29.66	< .001	1.16

	6 letters			29.43	< .001	1.16
Memory load effect (Retrieval)	3 > 6 letters	Higher upper alpha at 3 letters	Midline fronto-central-parietal	17.07	.006	.38
Brain-behavior association	5 letters	Higher upper alpha higher accuracy	Left fronto-central and occipital		≤ .044 (FDR)	OR = 1.08 - 1.18

Note. Topography summarizes significant electrode clusters. The values are the minimum and maximum values of each statistic (*t-sum*, *p*, and Cohen's *d*). In the brain-behavior association analysis, odds ratios (OR) reflect increased probability of correct responses associated with higher alpha power (false discovery rate-corrected *p*-values).

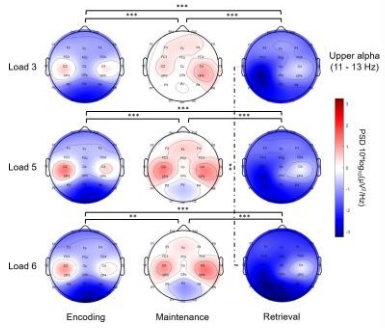

Figure 4. The absolute power of the upper alpha frequency band in each condition and working memory processing stage averaged across participants. The specific cluster statistic values and *p* values are in table 2. * *p* < .05; ** *p* < .01; *** *p* < .001.

4. Discussion

Sternberg's paradigm is widely regarded as a typical short-term memory task and is commonly used to investigate mnemonic capacities and stage-specific processing. In the present experiment, the probe appeared as a lowercase letter, requiring participants to transform it into its uppercase representation before comparing it to the memorized sequence. This additional transformation likely increased executive demands during retrieval and amplified the need for controlled comparison processes, particularly as string length increased. Consequently, task difficulty scaled with memory load, as confirmed behaviorally.

4.1. Behavioral Results

Behavioral performance confirmed the effectiveness of the load manipulation, with reduced accuracy and slower reaction times under higher memory load, validating expectations based on the load theory of attention, which states that an increase in working memory load impairs selective attention, thus producing more significant distractor interference [36]. Selective attention can facilitate target processing at both early perceptual and post-perceptual processing stages, wherein working memory can be functionally dissociated based on the type of information maintained within this online system [31]. The behavioral results confirmed that increasing memory load reduced accuracy and slowed response times, consistent with capacity-limited models of working memory [37,2].

4.2. Theta Oscillations

Theta activity reached its highest magnitude during retrieval, showing a retrieval-related enhancement, with additional load-dependent modulation during maintenance. This pattern was consistent across memory loads, although load-dependent modulation emerged primarily during maintenance. Our results suggest that in the present task, theta was more closely related to retrieval, decision-making, and executive coordination than to encoding or maintenance, as prior findings reported in the introduction.

Frontal-midline theta oscillations increase in amplitude during cognitive control tasks, and this increase has been associated with greater cognitive effort [38]. In the present experiment, though, while WM processing occurred, the relative increase in theta power across the time domain may not indicate successive effortful WM stages. It may be due to the distinct participation of several brain regions, such as the hippocampus and entorhinal cortex, during WM encoding and retrieval stages [39,40]. In addition, the influence of concurrent cognitive and perceptual processes, such as attention and task engagement, may underlie the variations in theta power observed from encoding to retrieval [41].

The main claim is that the stage-dependent increase in theta shows these oscillations reflect retrieval and decision-making processes, not just general cognitive effort [42]. However, the data do not allow direct inference about the exact mechanisms. Importantly, the fronto-central distribution of this effect aligns with the role of frontal-midline theta in cognitive control and goal-directed behavior [1,43-45]. Frontal-midline theta oscillations are also linked to working memory performance and capacity [23,46].

Importantly, increased theta power during retrieval in the lowest memory load condition predicted faster reaction times, indicating behavioral relevance of this oscillatory activity. This association supports the view that theta facilitates efficient access to stored representations and coordination of executive processes during response execution.

Although hippocampal-cortical mechanisms have been proposed in prior research [47], the present scalp EEG findings are more parsimoniously interpreted as reflecting large-scale fronto-parietal coordination during retrieval rather than direct evidence of deep-source activity. Probe-related theta likely reflects integrated mnemonic and decision-related processes required for memory-guided responding.

It is important to emphasize that the use of lowercase probes was intended to reduce reliance on direct visual matching strategies. However, this design likely introduced additional executive processes, including case transformation, rule application, and decision-related processing. Therefore, the increased theta activity observed during retrieval may reflect a combination of memory retrieval and executive control processes rather than retrieval alone. This interpretation is consistent with prior work linking frontal theta activity to executive control and decision-making processes [43,48].

4.3. Alpha Oscillations

In contrast to theta, alpha activity showed a robust, highly consistent stage effect across both lower and upper alpha bands. Alpha power was significantly higher during maintenance than during encoding and retrieval across all load levels.

These findings are consistent with, though not definitive evidence for, inhibitory gating accounts of alpha oscillations. Increased alpha power during maintenance likely reflects active suppression of irrelevant perceptual input in order to protect internally maintained representations. It has been reported an increase in alpha power modulated by the perceptual load in working memory [49,50], rather than passively reflecting cortical idling, alpha might implement top-down gating mechanisms that stabilize mnemonic content [51], probably focusing efforts to prevent reorienting to irrelevant stimulation during goal-driven, top-down behavior [52].

Notably, alpha did not exhibit a global load effect in our experiment. However, occipital lower alpha power was reduced under higher load during maintenance (in agreement with previous reports on this effect [53]), suggesting that increased mnemonic demand may partially diminish inhibitory gating in posterior sensory regions. Furthermore, upper alpha power significantly predicted accuracy under moderate load conditions. This association across encoding, maintenance, and retrieval suggests that alpha-mediated inhibitory control contributes directly to successful task performance when working memory operates near capacity limits.

4.4. Differential Stage-Specific Modulation of Theta and Alpha

The most important contribution of the present study is the demonstration of a functional dissociation between theta and alpha oscillations across temporally separated working memory stages.

The results show that theta activity was sensitive to both stage and load, peaking during retrieval and predicting response speed, while alpha activity was primarily stage-dependent, peaking during maintenance and predicting accuracy under moderate load. These findings suggest that theta and alpha oscillations subserve partially independent, but complementary mechanisms. Theta reflects executive integration and retrieval-related coordination, and alpha reflects inhibitory stabilization and protection of maintained representations.

By using a Sternberg paradigm that temporally separates encoding, maintenance, and retrieval, the present study clarifies inconsistencies in prior n-back literature where overlapping processes may have obscured stage-specific oscillatory dynamics.

Although we initially hypothesized a progressive decrease in alpha power across stages, the observed increase during maintenance suggests that alpha oscillations play an active regulatory role in stabilizing working memory representations rather than reflecting reduced cognitive engagement.

5. Conclusions

Taken together, the present findings reveal stage-specific and frequency-specific oscillatory signatures of working memory, namely: i) retrieval engages theta-mediated executive coordination; ii) maintenance recruits alpha-mediated stabilization mechanisms; iii) distinct oscillatory processes depending on task demand and memory load level underlie behavioral performance. These results highlight the importance of distinguishing frequency sub-bands and processing stages when interpreting oscillatory dynamics in working memory.

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