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Oscillatory delta and theta frequencies differentially support multiple items encoding to optimize memory performance during the digit span task

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ABSTRACT

The human brain has limited storage capacity often challenging the encoding and recall of a long series of multiple items. Different encoding strategies are therefore employed to optimize performance in memory processes such as chunking where particular items are 'grouped' to reduce the number of items to store artificially. Additionally, related to the position of an item within a series, there is a tendency to remember the first and last items on the list better than the middle ones, which calls the "serial position effect". Although relatively well-established in behavioral research, the neuronal mechanisms underlying such encoding strategies and memory effects remain poorly understood. Here, we used event-related EEG oscillation analyses to unravel the neuronal substrates of serial encoding strategies and effects during the behaviorally controlled execution of the digit span task. We recorded EEG in forty-four healthy young-adult participants during a backward digit span (ds) task with two difficulty levels (i.e., 3-ds and 5-ds). Participants were asked to recall the digits in reverse order after the presentation of each set. We analyzed the pattern of event-related delta and theta oscillatory power in the time-frequency domain over fronto-central and parieto-occipital areas during the item (digit) list encoding, focusing on how these oscillatory responses changed with each subsequent digit being encoded in the series. Results showed that the development of event-related delta power evoked by digits in each series matched the 'serial position curve', with higher delta power being present during the first, and especially last, digits as compared to digits presented in the middle of a set, for both difficulty levels. Event-related theta power, in contrast, rather resembled a neural correlate of a chunking pattern where, during the 5-ds encoding, a clear change in event-related theta occurred around the third/fourth positions, with decreasing power values for later digits. This suggests that different oscillatory mechanisms linked to different frequency bands may code for the different encoding strategies and effects in serial item presentation. Furthermore, recall-EEG correlations suggested that participants with higher fronto-central delta responses during digit encoding showed also higher recall scores. The here presented findings contribute to our understanding of the neural oscillatory mechanisms underlying multiple item encoding, directly informing recent efforts towards memory enhancement through targeted oscillation-based neuromodulation.

1. Introduction

Despite the human brain's remarkable complexity and computational resources, it has a restricted capacity when it comes to working memory (Constantinidis & Klingberg, 2016; Cowan, 2001; Marois & Ivanoff, 2005). The human brain has limited storage capacity directly related to how information is encoded and represented in the brain. The mere position of an element within a series and/or the overall number of items to be stored affect these capacity limits and the chance of successful recall (Constantinidis & Klingberg, 2016; Murre & Dros, 2015). Furthermore, the number of items to be held and their position within a sequence of items determine how to best encode such lists to optimize memory storage (Saito et al., 2008; Thalmann et al., 2019). A well-established example of how the position of an item in a list can affect the memory processes is the "serial position effect" (SPE) (Feigenbaum & Simon, 1962; Murdock, 1962; Murre & Dros, 2015). The SPE describes the propensity to remember the first and last items on a list more efficiently than the middle ones. In addition to such memory effects of serial position, there is also an encoding strategy to optimize memory perfor-

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mance. This encoding strategy is known as “chunking” (Ericsson et al., 1980; Shiffrin & Nosofsky, 1994), a strategy where distinct items are ‘grouped’ to artificially reduce the number of items in a list in order to retain more of them. Chunking may be a common approach for encoding episodic information, and it is an effective way to reduce the buildup of error inherent in long sequences by reducing the amount of information to be recalled (Buzsáki & Moser, 2013; Cowan, 2001, 2005, 2010; Wickelgren, 1999).

Despite well-established behavioral demonstrations of such memory effects and encoding strategies from a research tradition that began more than a century ago (i.e., Ebbinghaus, 1885; Jevons, 1871), their underlying neural mechanisms remain less fully understood. There are a limited number of event-related electroencephalography (EEG) studies focusing on the above-mentioned encoding processes. In EEG literature, several studies studied “chunking" in the scope of language processing (Bonhage et al., 2017; Gilbert et al., 2014, 2015). According to these studies, delta-theta oscillatory responses (Bonhage et al., 2017), as well as N400 and P300 components (Gilbert et al., 2014), may reflect chunking-related encoding during language processing. Additionally, Nogueira et al (2015) showed increased late positive slow waves during the encoding of the words when the items were chunked (Nogueira et al., 2015) compared to a control condition. On the other hand, the serial position effect was reflected mostly by the late positive event-related potentials (ERP), with the effect depending on stimulus modality (Azizian & Polich, 2007; Patterson et al., 1991). To our knowledge, there are only a few studies investigating neural oscillations underlying the SPE directly (Jensen & Lisman, 1998; Sederberg et al., 2006). While Jensen & Lisman (1998) focused on the role of theta oscillations in the serial position effect, Sederberg et al. (2006) showed that the posterior gamma (at early serial positions) and widespread slow oscillatory responses (for later serial positions) may reflect the serial position effect. These relatively few event-related EEG studies nonetheless clearly demonstrate that the EEG is a tool and method that has been used successfully before to investigate the processes of chunking and SPE in memory research.

Although these limited numbers of pioneering studies in which the effect of item position and item number on encoding processes were studied with the event-related EEG method, results were not consistent, and we found little recent work explicitly addressing these mechanisms. Given the relevance of serial encoding for our everyday cognition (remembering a shopping list), this seems surprising. Intriguingly, noninvasive neuromodulation techniques have recently been used successfully to specifically target cognitively relevant brain oscillations to enhance memory performance (Grover et al., 2022; Aktürk et al., 2022). Therefore, an in-depth understanding of brain oscillations underlying encoding processes related to serial position effect and chunking might directly inform such developments towards cognitive neuroenhancement in healthy populations as well as benefit intervention in pathologies in which encoding is disrupted.

To this end, we here decided to focus on slow oscillatory EEG responses (i.e., delta and theta), since they are widely associated with cognitive processes such as attention and memory. Delta responses have mostly been associated with immediate memory mechanisms, decision-making, and attention allocation processes (Başar-Eroglu et al., 1992; Ergen et al., 2008; Harper et al., 2017; Polich & Kok, 1995; Sutton et al., 1965). For example, studies using the oddball paradigm report an amplitude increase at delta frequency when the participants perceive a target stimulus, necessitating the perception and attention processes (Başar-Eroglu et al., 1992; Demiralp et al., 1999; Ergen et al., 2008). Considering this link between delta responses and immediate memory and attention mechanisms, which are basic information-processing mechanisms in working memory, we might expect that the delta response will be affected by the serial positions of items in a list and therefore related to the serial position effect (Feigenbaum & Simon, 1962). Theta responses, on the other hand, are mostly associated with working memory capacity and thereby with the number of items that should be remembered, as also shown by research on theta-gamma coupling (Goodman et al., 2018; Herweg et al., 2020; J. E. Lisman & Jensen, 2013; J. Lisman & Idiart, 1995). Theta oscillations take part in managing successive inputs by holding items within a single theta cycle (Buzsáki, 2005; Herweg et al., 2020). Therefore, one might hypothesize that “chunking” could be reflected by theta activity rather than delta.

Here, we analyzed the pattern of event-related delta and theta power in the time-frequency domain over bilateral fronto-central and parieto-occipital areas during the digit span backward working memory task. In this task, digits were presented to the participants sequentially in two different list lengths: 3 digit span (3-ds) and 5 digit span (5-ds), respectively. After each set of digits, the participants were asked to recall the digit sets in reverse order. In order to disentangle possible encoding mechanisms and memory effects reflected by delta-theta slow brain oscillations, the encoding phase of the task, during the item (digit) representation, was analyzed.

2. Materials and Methods

This study is part of a larger study investigating EEG-informed theta tACS after effects. Here, we used the pre-tACS EEG data of the participants that were recorded during the working memory task. These participants did not have tACS during or before they performed this task, and they were not prepared for tACS yet; therefore, the current EEG results and preparation are indistinguishable from an isolated EEG experiment. However, we think it is important to mention that prior to the digit span task, as a part of the larger tACS study design, a neuropsychological battery and visual and auditory memory tasks were administered to participants for approximately one hour (for details please see; Aktürk et al., 2022).

2.1. Participants

A total of 44 (33 females) right-handed, educated (mean years of education (SD): 16.3 (±2.7)), healthy young-adult (mean age (SD): 24.4 (±4.8)) subjects were included in the study. All participants had normal or corrected-to-normal vision and no specified hearing impairment. Participants with symptoms or history of psychiatric or neurological disorders and psychiatric or neurological medication usage were not included in the study.

Participants provided written informed consent, and there was no compensation for participation as indicated in the written informed consent. The study was approved by the Istanbul Medipol University Ethics Committee (No: 10840098-604.01.01-E.18575).

2.2. Experimental Design and Task Procedure

The digit span backward task was prepared and presented via E-prime software (Psychology Software Tools Inc., Pittsburgh, PA). This task mainly measures the working memory abilities of the subjects. Here, we presented the task in the two different difficulty levels, namely, the 3-digit span (3-ds) set and the 5-digit span set (5-ds) during the EEG recording. These levels were always presented in the same order (first: 3-digit span sets and then 5-digit span sets). A total of 30 different digit sets were presented during the task in each difficulty level. Digit sets were presented in the pseudorandom order across participants. During the encoding phase of the task, the digits appeared on the screen sequentially for each digit span set, namely 5 digits were presented for a 5-ds set and 3 digits were presented for a 3-ds set. Stimulation time per digit was 900 ms, and interstimulus interval was 600 ms between the digits in a set. The encoding phase was followed by the recall phase. Before the task, participants were instructed to pay attention to approaching stimuli (learning/encoding phase) and recall a set of digits in reverse order to log answers via a keyboard on the answer screen following each digit set (recall phase). The answer screen was presented 600 ms after the offset of the last digit in the set and disappeared after the participant

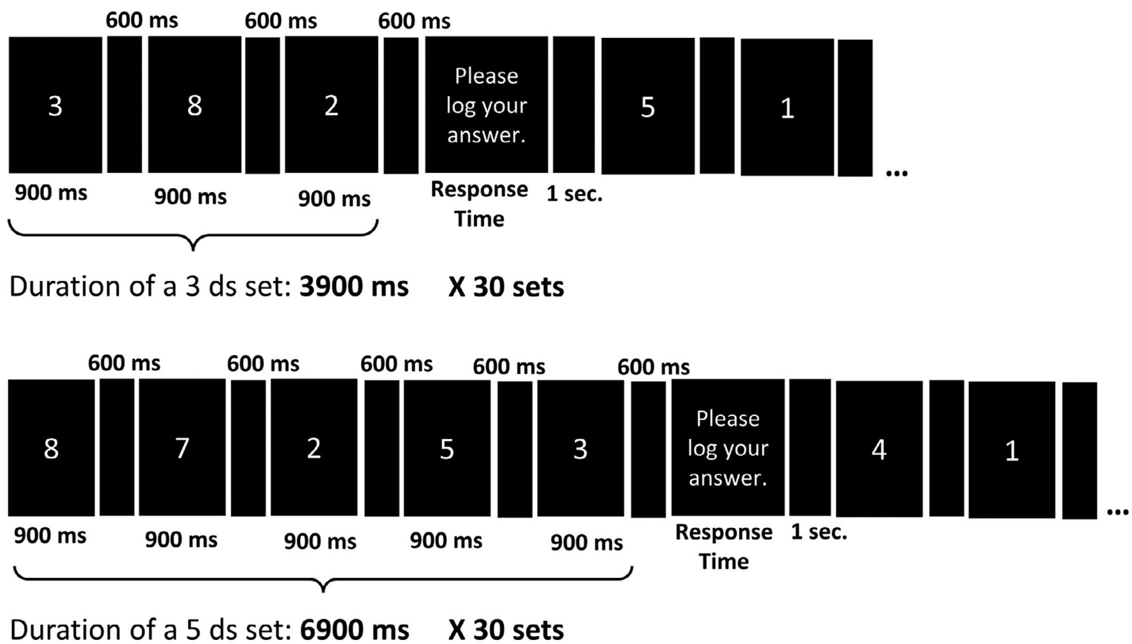

Fig. 1. Task procedure. The representations of the applied digit span backward task during the EEG recordings (3ds set above and 5ds set below). ds: digit span, ms: millisecond, sec.: second

entered and confirmed their answer by pressing "enter"; or the answer screen disappeared after a maximum of 7 seconds for 3 digits set; 15 seconds for 5 digits set. A 1-second black wait screen was presented after the answer screen. The design of the digit span backward paradigm is shown in Fig. 1.

Each digit span set entered correctly to the answer screen for a presented digit span set was considered a "correct answer". Accordingly, for a participant, the total number of correct answers were calculated as a "recall score" for each difficulty level separately. The maximum recall score achievable is 30 as this is the amount of sets presented for each difficulty level.

To ensure that participants understood the tasks, right before the task, a short version of the 3-digit span task was given as the trial. The same procedure was applied in the actual task with the different stimuli from the actual task in the trial. During the trials, 3 different 3-ds sets were presented.

The digits were shown on a 47.5 × 26.8 cm size monitor with a refresh rate of 60 Hz that was placed 90 cm away from the participants. Digits were presented in the center of the screen. The approximate visual angle for the stimuli (each digit) measured 3 degrees horizontally and 3.3 degrees vertically.

2.3. EEG Recording

EEG was recorded from Fp1, Fp2, F7 F3, Fz, F4, F8, Ft7, Fc3, Fcz, Fc4, Ft8, Cz, C3, C4, T7, T8, Tp7, Cp3, Cpz, Cp4, Tp8, P3, Pz, P4, P7, P8, O1, Oz and O2 electrodes with "BrainCap with Multitrodes" model cap (EasyCap GmbH, Germany) with 32 electrodes placed based on the international 10–20 system. Two linked earlobe electrodes (A1 + A2) served as references. The electrooculogram (EOG) was recorded at the left eye's medial upper and lateral orbital rim. The impedance of all electrodes was kept below approximately 10 kΩ. The EEG was amplified by means of a BrainAmp MR plus 32-channel DC system machine (Brain Product GmbH, Germany) with band limits of 0.01–250 Hz and digitized online with a sampling rate of 500 Hz. The participants were sitting in a dimly lit and shielded room during EEG recordings.

2.4. EEG Analysis

The preprocessing steps and further analyses of the event-related EEG data were performed in Brain Vision Analyzer software (BVA). For the event-related EEG data preprocessing steps were as follows; I) data were filtered between 0.1 Hz to 60 Hz, II) independent component analysis was applied to remove eye-movement related artifacts, III) data were segmented into 5.5-second (1 second before and 4.5 seconds after the stimulus) and 8.5-second epochs (1 second before and 7.5 seconds after the stimulus) for 3-ds and 5-ds set tasks, respectively, IV) manual artifact rejection was performed over the segmented data. EEG data were not re-referenced since the online referencing scheme remained/unchanged (two linked earlobe electrodes (A1 + A2)) for the further EEG analyses.

While the importance of frontal and central areas is shown in the memory processes (i.e., Jensen & Tesche, 2002; Nogueira et al., 2015) the importance of parietal and occipital areas in number perception is known from the literature (i.e., Hesse et al., 2017; Rinsveld et al., 2020), as mentioned in the Introduction; therefore, here, anterior (fronto-central) and posterior (parieto-occipital) electrode pairs were chosen for the analysis. Accordingly, the further EEG analysis was run over two locations, namely 8 electrodes (fronto-central: F3, F4, C3, C4, parieto-occipital: P7, P8, O1, O2).

Over the preprocessed data, event-related analyses in the time-frequency domain were applied by the Gabor normalized complex Morlet Wavelet Transform (WT) with 4 cycle wavelet widths for the 1-15 Hz frequency range. The determined frequency range (1-15 Hz) was subdivided into 60 bins (the "frequency steps" parameter was set as "60"), scaled logarithmically (the "Logarithmic Steps" option was selected). The WT was calculated in each frequency bin. Analysis was performed for both 3-ds and 5-ds tasks separately (over 5.5 and 8.5 seconds length epochs, respectively).

In the event-related power analysis, as a normalization, the values were converted to the decibel (dB) scale. In this decibel normalization, pre-stimulus activity in the time window -500 ms to the -200 ms was used as the reference interval in time. The event-related power was calculated by averaging single trials to which WT was applied to reach total power (evoked+induced power).

Stimulation time per digit was 900 ms and ISI was 600 ms between digits presented in a set (see Method section for detail of the task design). And wavelet analysis was not applied for each digit separately but for a set of digits, which means we used 5.5 second time interval for the 3-ds set and 8.5 second time interval for the 5-ds. For obtaining event-related delta and theta responses values for each digit we averaged values within the *"determined time"* and frequency (Delta:1-3.5 Hz and theta: 4-8 Hz) window. The determined time window was 20-700 ms for delta and 50-250 ms for theta, from digit onset to digit offset for each digit presented in a set. The sum values of the specified time and frequency window were divided by the total number of data points in the chosen time-frequency interval (point mean normalization), producing average values; and these values were used in the statistical analyses.

2.5. Statistical Analysis

Statistical analyses were performed with IBM SPSS Statistic 22 Software (IBM Corp., Armonk, N.Y., USA), R Statistical Software (Foundation for Statistical Computing, Vienna, Austria), and Jamovi (The jamovi project, 2021) software.

For the statistical analysis of the delta event-related power analysis, to test the serial position effect, the positions of the digit in a set were added as a within-subject factor as well as location and hemisphere factors. Therefore, three-way (2 × 2 × 3) repeated measures ANOVA was performed. The location (Fronto-Central, Parieto-Occipital), hemisphere (Right, Left), and position (First, Middle(s), Last) were the within-subjects factors in the design. In the 5-ds task, for the "middles" level of position factor, second, third, and fourth digits' delta responses were averaged.

For the statistical analysis of the theta event-related power analysis, repeated-measures ANOVA was run only to see the topographical distribution over the selected locations and hemispheres. Therefore, 2-by-2 repeated-measures ANOVA was performed. The location (Fronto-Central, Parieto-Occipital) and hemisphere (Right, Left) were the within-subjects factors in the design. Additionally, to evaluate the possible chunking strategy, as an encoding strategy reflected by theta responses, we employed the findchangepts algorithm used for change point detection in MATLAB (Killick et al., 2012; Lavielle, 2005). The algorithm finds where the abrupt change occurs across the signal. This function was here used to find the change points among up to four points (since the task has the 5 items in a set, leading to 4 changes) where the changes in root-mean-square level were most pronounced. Then, the Chi-Square test was used to statistically test the distribution of the detected change points across the possible four change points. This would reveal whether, across participants, there was statistically significant consistency at the moment in time where the change in event-rated power was most pronounced (null hypothesis; all change points equally likely, so no consistency). The change point detection function results allow us to see where the change happened; however, we cannot know the direction of the changes, and the change could have happened in both directions. Therefore, following the change point analysis, the repeated measure ANOVA with position (first, second, third, fourth, last) factor was run to evaluate the direction of the power changes across the positions.

In order to reveal possible EEG-behavior interaction, a bivariate linear correlation (Pearson correlation, 2-tailed) analysis between behavioral scores and EEG data was used. As behavioral data, only 5-ds task scores were used in the correlation analysis since there was not enough variation in the 3-ds task scores due to its ease. As the EEG data, delta and theta mean power values of each response to the digits in a set were used separately over fronto-central and parieto-occipital areas.

The significance threshold was set at $p < 0.05$. Greenhouse Geisser corrected p values reported for the ANOVA analysis. For post-hoc comparisons, Holm adjusted p values were reported.

3. Results

3.1. Behavioral Results

In the digit span backward working memory task, a participant's total correct responses were determined as a "recall score" out of 30 points for each difficulty level independently (3-ds and 5-ds) since 30 sets were presented for each difficulty level. In order to see the effect of list length on task performance of individuals, a paired samples t-test was conducted. As expected, the results indicate that participants showed higher performance on 3-ds ($M = 27.7$, $SD = 2.05$) condition compared to the 5-ds ($M = 23.6$, $SD = 4.68$) ($t(36.0) = 5.26$, $p < .001$). Considering the study's participant population (educated, healthy, young-adult), it was quite expected that they would have a very high mean score for the 3-ds task.

3.2. EEG Results

3.2.1. Delta Power Results

We used complex Morlet Wavelet Transform to obtain event-related delta (1-3.5 Hz) oscillations in the time-frequency domain in response to each digit in the digit span backward working memory task. The position of the digits in a digit set was considered as a factor to assess the serial position effect on delta responses.

3.2.1.1. Three Digit Span Results. A 2 (Location: Fronto-Central, Parieto-Occipital) X 2 (Hemisphere: Right, Left) X 3 (Position: First, Middle, Last) repeated measures ANOVA results with a Greenhouse-Geisser correction indicated that there were main effects of digit Position ($F(1.40, 60.21) = 24.95$, $MSe = 6.79$, $p < .001$, $\eta 2 = .37$) and electrode cluster (Location; ($F(1, 43) = 16.96$, $MSe = 4.17$, $p = .005$, $\eta 2 = .17$)) on event-related delta power. However, these main effects were dependent on the location and hemisphere, since there were significant location*position, hemisphere*position and location*hemisphere interactions. In the following paragraphs these interaction results were elaborated, respectively.

The ANOVA results indicated that there was an interaction between location and position factors ($F(1.76, 75.71) = 6.99$, $MSe = 1.22$, $p = .002$, $\eta 2 = .14$) (Fig. 2). We followed up this 2-way interaction by performing separate one-way repeated measure ANOVAs for the two locations (FC & PO) to see whether the expected position effect (u-shaped serial position curve) is location specific. Results showed that the position main effect was significant in both locations (in FC: ($F(1.45, 62.26) = 30.0$, MSe = 1.98, $p < .001$, $\eta 2 = .41$; in PO: ($F(1.51, 65.13) = 13.8$, MSe = 1.90, $p < .001$, $\eta 2 = .24$). Accordingly, in FC, pairwise comparisons showed that participants had lower power for the first digit position ($M = -.64$, $SD = .92$) than the last digit position ($M = .44$, $SD = 1.78$) ($t(86.0) = -4.23$, $p < 0.001$); and, they had lower power for the middle digit position ($M = -1.53$, $SD = 1.14$) than the first and last digit positions (first vs. middle, $t(86.0) = 3.50$, $p < .001$; last vs. middle, $t(86.0) = -7.73$, $p < .001$) (Fig. 2A, Fig. 5A). The similar pattern found in PO as well (first ($M = .13$, $SD = 1.01$) vs. middle ($M = -.80$, $SD = 1.46$), $t(86.0) = 3.65$, $p < .001$; last ($M = .51$, $SD = 2.09$) vs. middle, $t(86.0) = -5.11$, $p < .001$) except first-last digit difference ($t(86.0) = -1.45$, $p = .15$) (Fig. 2A, Fig. 5A).

The ANOVA results showed that there was also a significant interaction between position and hemisphere ($F(1.57, 67.30) = 7.43$, $MSe = 0.32$, $p = .003$, $\eta 2 = .15$). We followed up this 2-way interaction by performing separate one-way repeated measure ANOVAs for the two hemispheres (R & L) to see whether the expected position effect (u-shaped serial position curve) is hemisphere specific. Results showed that the position main effect was significant in both hemisphere (in L: ($F(1.31, 59.15) = 26.5$, MSe = 2.13, $p < .001$, $\eta 2 = .38$; in R: ($F(1.57, 67.39) = 21.0$, MSe = 1.42, $p < .001$, $\eta 2 = .33$). The post-hoc comparison analysis showed that in the left hemisphere, participants had a higher delta response for first ($M = -.32$, $SD = .86$) and last ($M = .56$,

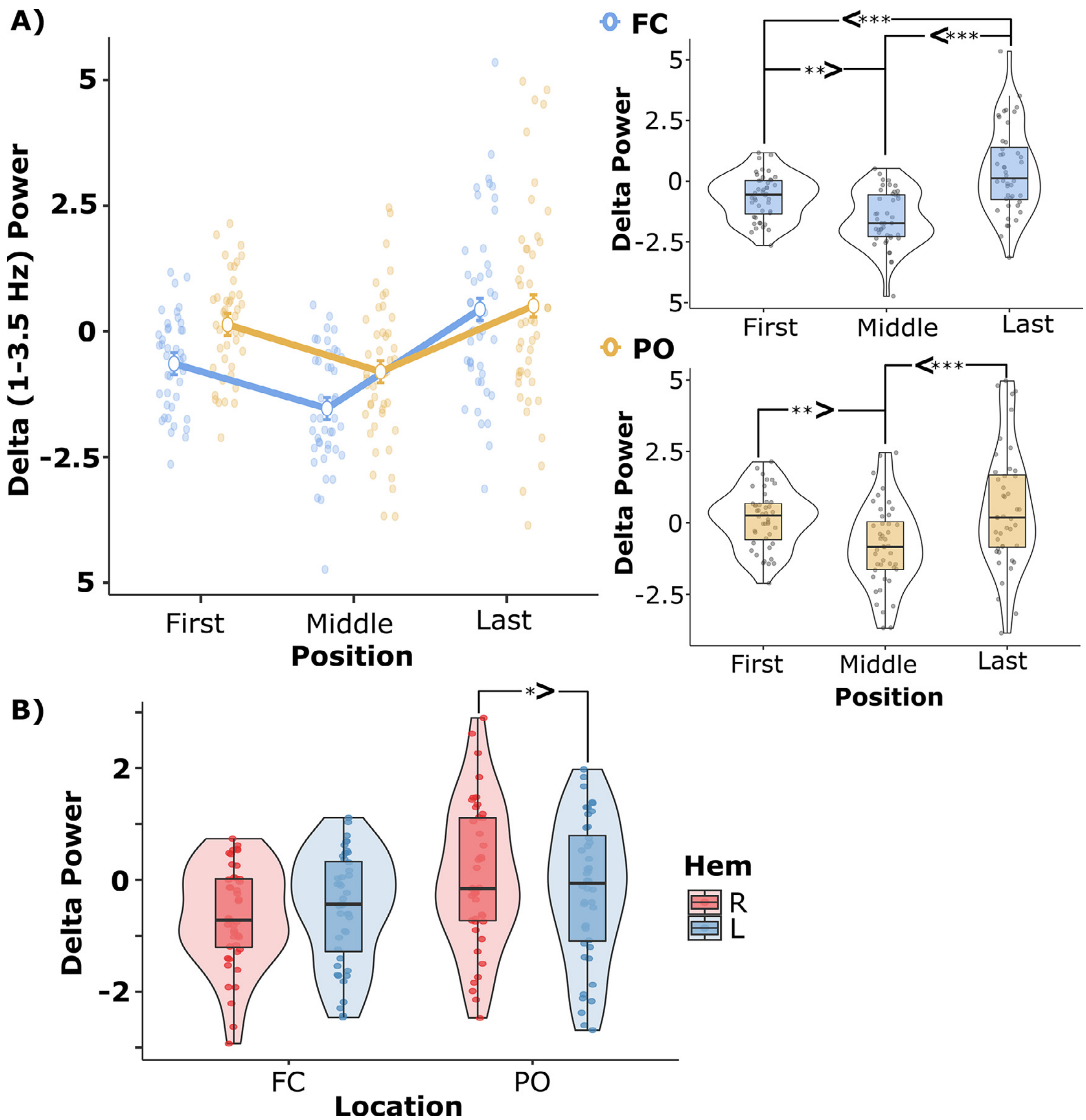

Fig. 2. The location*position and location*hemisphere plots for delta responses (1-3.5 Hz) in 3-ds backward task. A) The left plot shows the significant location*position interaction ($p = .002$). The right plots show the position effect for each location. In the FC, participants had lower power for the first digit position than for the last digit position ($p < 0.001$); and, they had lower power for the middle digit position than for the first and last digit positions (first vs. middle, $p = .004$; last vs. middle, $p < .001$). In the PO, participants had lower power for the middle digit position than the first and the last positions (first vs. middle, $p = .003$; last vs. middle, $p < .001$), and there was no difference between the delta response given to the first and last digit ($p = 0.59$). **B)** The plot shows the significant location*hemisphere interaction ($p < .001$). Participants had lower left PO power compared to the right PO ($p = 0.019$). Yet, there was no such hemispheric difference in the FC ($p = 0.17$). Hem: hemisphere, R: right, L: left, FC: fronto-central, PO: parieto-occipital. The error bars on box plots denote the standard error of the mean. Asterisks indicate statistical significance (*: $p \leq .05$, **: $p \leq .01$, ***: $p \leq .001$). Dots represent the observed scores.

SD = 1.86) positions than the middle (M = -1.27, SD = 1.18) (first vs. middle, $t(86.0) = 3.78$, $p < .001$; last vs. middle, $t(86.0) = -7.28$, $p < .001$) and also had a higher delta response for the last position than the first ($t(86.0) = -3.50$, $p < .001$) (Fig. 5A). The same pattern was seen in the right hemisphere; participants had a higher delta response for the first (M = -.19, SD = .81) and last (M = -.38, SD = 1.69) positions than the middle (M = -1.06, SD = 1.11) (first vs. middle, $t(86.0) = 3.89$, $p < .001$; last vs. middle, $t(86.0) = -6.43$, $p < .001$), and had a higher delta response for the last position than the first ($t(86.0) = -2.54$, $p = .013$) (Fig. 5A).

As can be seen from the follow-up analyses of the interactions, the pattern (serial position curve) seen in the position main effect is preserved despite significant interactions (Fig 2A) (see Supplementary Fig. 1-7 for the individual level quadratic relationship model and distribution of the digit position-delta power values.).

In addition, the ANOVA results showed that there was an interaction between location and hemisphere ($F(1, 43) = 16.96$, $MSe = .32$, $p < .001$, $\eta 2 = .28$) (Fig. 2B). The post-hoc analysis demonstrated that participants had lower left PO (M = -.18, SD = 1.27) power compared to the right PO (M = .074, SD = 1.28) ($t(75.5) = 2.93$, $p = 0.019$) (Fig. 5A). Yet, there was no such hemispheric difference in the FC ($t(75.5) = -1.62$, $p = 0.17$).

3.2.1.2. Five Digit Span Results. A 2 (Location: Fronto-Central, Parieto-Occipital) X 2 (Hemisphere: Right, Left) X 3 (Position: First, Middles, Last) repeated measures ANOVA results with a Greenhouse-Geisser correction revealed that there was a main effect of position ($F(1.38, 56.72) = 22.90$, $MSe = 9.51$, $p < .001$, $\eta 2 = .36$). However, this effect was dependent on the location and hemisphere factors since there is a significant location*hemisphere*position interaction ($F(1.88, 77.27) = 4.53$, $MSe = 0.12$, $p = .02$, $\eta 2 = .10$) (Fig. 3). We followed up this 3-way

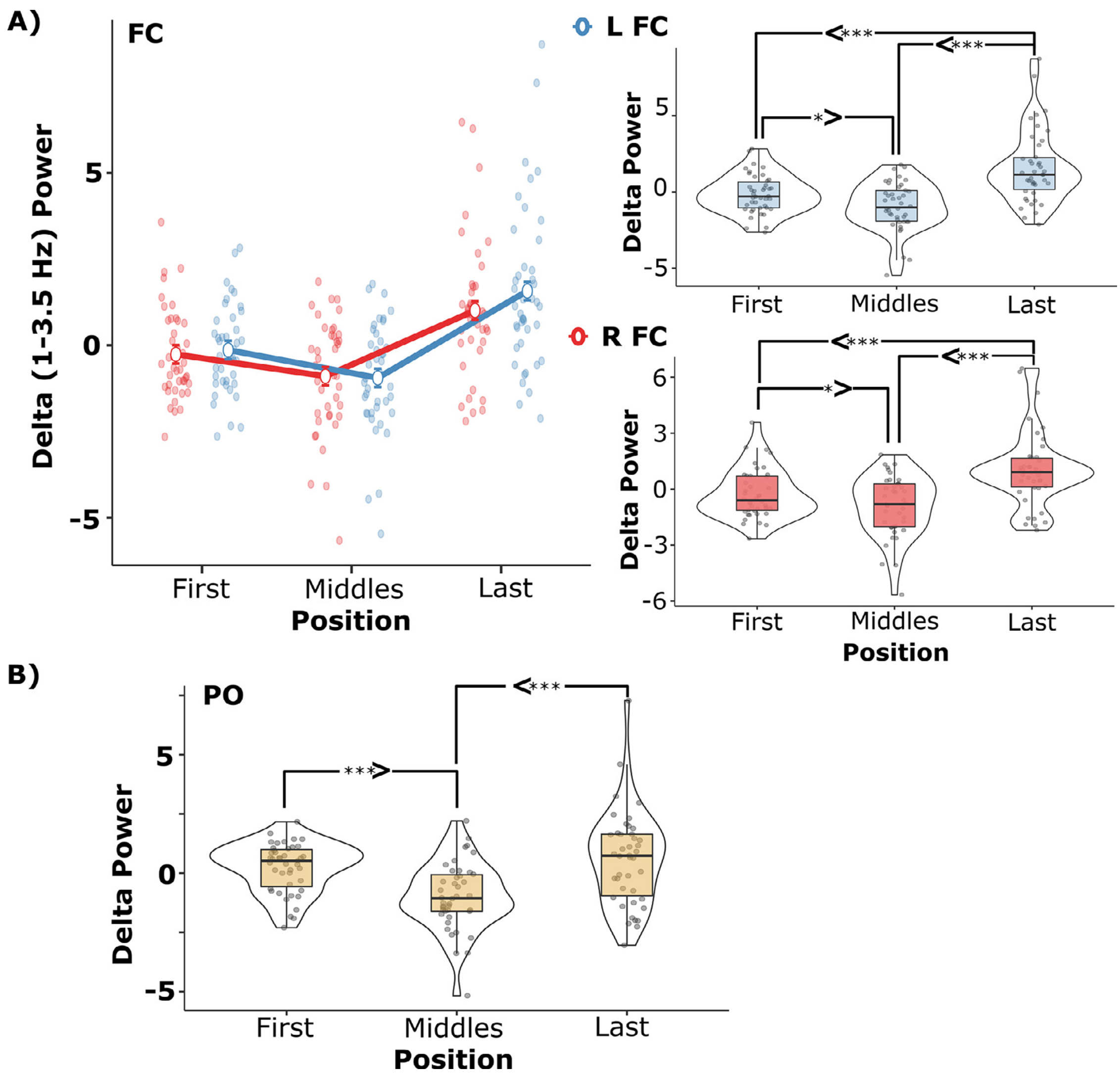

Fig. 3. The plots of the hemisphere*position interaction in the FC (A) and the position effect in the PO (B) for delta responses (1-3.5 Hz) in the 5-ds backward task. A) The hemisphere*position interaction was significant in the FC ($p < .001$), and in the follow-up analyses position main effect was found significant for both hemispheres (left FC, $p < .001$; right FC, $p < .001$). Pairwise comparisons showed that in left FC, participants had higher power for the first and last digits than middle (first vs. middle, $p = .02$; middle vs. last, $p < .001$), and the last digit elicited higher power than the first ($p < .001$). The same pattern was observed in right FC as well; participants had higher power for the first and last digits than middle (first vs. middle, $p = .04$; middle vs. last, $p < .001$), and the last digit had higher power than the first ($p < .001$). **B)** In the PO, the position main effect was significant ($p < .001$). Pairwise comparisons showed that participants had higher power for the first and the last digit position than the middle position (first vs. middle, $p < .001$; middle vs. last, $p < .001$) L: left, R: right, FC: fronto-central, PO: parieto-occipital. The error bars on box plots denote the standard error of the mean**.** Asterisks indicate statistical significance (*: $p \leq .05$, **: $p \leq .01$, ***: $p \leq .001$). Dots represent the observed scores.

interaction by performing separate 2 × 2 ANOVAs for the two locations (FC & PO) to determine for which locations and hemispheres we can see the expected position effect (u-shaped serial position curve). Results showed that the hemisphere*position interaction was significant in the FC ($F(1.44, 59.19) = 13.02$, $MSe = 0.22$, $p < .001$, $\eta 2 = .24$). And when we followed up this 2-way interaction with the one-way repeated measures ANOVAs for each hemisphere (Left & Right), the position main effect was found significant for both hemispheres (left FC: $F(1.39, 57.04) = 28.5$, $MSe = 3.52$, $p < .001$, $\eta 2 = .41$; right FC: $F(1.55, 63.51) = 20.7$, $MSe = 2.48$, $p < .001$, $\eta 2 = .34$). Accordingly, pairwise comparisons showed that in left FC participants had higher power for the first ($M = -.14$, $SD = 1.27$) and last digits ($M = 1.58$, $SD = 2.35$) than middle ($M = -.95$, $SD = 1.58$) (first vs. middle, $t(82.0) = 2.37$, $p = .02$; middle vs. last, $t(82.0) = -7.39$, $p < .001$), and last digit elicited higher power than first ($t(82.0) = -5.08$, $p < .001$) (Fig. 3, Fig. 5B). Same pattern observed in right FC as well; participants had higher power for the first ($M = -.26$, $SD = 1.31$) and last digits ($M = 1.01$, $SD = 1.98$) than middle ($M = -.90$, $SD = 1.62$) (first vs. middle, $t(82.0) = 2.21$, $p = .04$; middle vs. last, $t(82.0) = -6.32$, $p < .001$), and last digit had higher power than first ($t(82.0) = -4.21$, $p < .001$) (Fig. 3, Fig. 5B). When we look at the PO, we found that not the position*hemisphere interaction ($F(1.88, 76.90) = 2.77$, $MSe = 0.17$, $p = .07$, $\eta 2 = .06$) but the position main effect was significant ($F(1.42, 58.20) = 17.45$, $MSe = 4.62$, $p < .001$, $\eta 2 = .30$). The results of the post-hoc analysis for the main effect of position demonstrated that participants had higher power for the first (M = .23, SD = 1.04) and last (M = .58, SD = 2.00) digit position than the middle position (M = -.99, SD = 1.43) (first vs. middle, $t(82.0) = 4.38$, $p < .001$; middle vs. last, $t(82.0) = -5.62$, $p < .001$) (Fig. 3, Fig. 5B).

As for the delta 3-ds statistical results, we also here revealed that the pattern seen across digit positions is largely preserved despite significant interactions (see also Supplementary Fig. 8-17 for the individual level quadratic relationship model and the distribution of the digit position-delta power values).

In addition, Linear Mixed-Effects Models analysis was performed to investigate the continuous quadratic distributions of "digit position" in both 3-ds and 5-ds delta power responses. The models indicated that there were quadratic relationships between delta power values and digit positions. The results of these models were significant for both, the averaged data (all locations & hemispheres) and for each location and hemisphere separately (all *ps* $< .0001$). We included the figures of distributions, model results, and analysis results in the Supplementary Materials.

3.2.2. *Theta Power Results*

We used the complex Morlet Wavelet Transform to obtain event-related theta (4-8 Hz) oscillations in the time-frequency domain, in response to each digit in the digit span backward working memory task. Both 5 and 3-ds tasks were investigated in terms of locations (FC & PO) and hemispheres (LH & RH) with 2-by-2 ANOVA. Furthermore, theta responses in the 5-ds task were evaluated for chunking strategy. For this purpose, changepoint (cp) detection analysis was applied to find where the most significant theta power change happened during 5-ds (between the possible four transitions) in the root-mean-square level. Then, a Chi-Square test was used to evaluate the uniformity or lack thereof of the cp distribution across the four possible change points (5 digits results in 4 transitions between digits and their event-related theta responses and therefore 4 changepoints). Subsequently, repeated measures ANOVA were employed with the position factor to interpret the direction of the changes happening at the cp.

3.2.2.1. Three Digit Span Results. For investigating power changes of participants at theta frequency for three digit span conditions across the locations and hemispheres, we performed a 2 (Location: Fronto-Central, Parietal-Occipital) X 2 (Hemisphere: Right, Left) repeated measures ANOVA with a Greenhouse-Geisser correction. There was a main effect of the hemisphere ($F(1, 43) = 8.38$, $MSe = 0.69$, $p = .006$, $\eta 2 = .16$). The post-hoc analysis of this main effect demonstrated that participants had higher power at the right hemisphere ($M = .64$, $SD = 1.33$) than the left ($M = .28$, $SD = 1.26$) ($t(43.0) = 2.89$, $p = .006$) (Fig. 5A). In addition to these, the main effect of location was significant ($F(1, 43) = 30.79$, $MSe = 4.89$, $p < .001$, $\eta 2 = .42$). The pairwise comparison indicated that participants had higher power in the PO ($M = 1.38$, $SD = 2.05$) than FC ($M = -.46$, $SD = 1.13$) ($t(43.0) = -5.55$, $p < .001$) (Fig. 5A).

3.2.2.2. Five Digit Span Results. Another 2 (Location: Fronto-Central, Parieto-Occipital) X 2 (Hemisphere: Right, Left) repeated measures ANOVA with a Greenhouse-Geisser correction was performed for investigating power changes of participants at theta frequency for five digit span conditions. The results indicated that there were significant main effects of hemisphere ($F(1, 41) = 17.47$, $MSe = 0.35$, $p < .001$, $\eta 2 = .26$) and location ($F(1, 41) = 15.03$, $MSe = 3.52$, $p < .001$, $\eta 2 = .27$), however, there was also a significant location*hemisphere interaction ($F(1, 41) = 4.64$, $MSe = 0.39$, $p = .037$, $\eta 2 = .10$). Follow-up post-hoc analysis demonstrated that the right PO ($M = .76$, $SD = 2.09$) had higher power than the left ($M = .21$, $SD = 1.78$) ($t(81.7) = -4.18$, $p < .001$) while there was no such a hemispheric difference in the FC ($t(81.7) = -1.05$, $p = .30$).

To investigate the theta power results for the chunking strategy in the five digit span task performances of participants, we used the findchangepts algorithm in MATLAB. As we explained in the methods section, this algorithm finds where the theta power values change most strongly among the four transitions between the five digits. The results of this algorithm demonstrated that 22 (%52,4) participants had the biggest change at the third digit (meaning the transition between digits 2 and 3), and 20 (%47,6) participants had the biggest change at the fourth digit (meaning the transition between digits 3 and 4), while no participant showed the biggest change at digits 2 or 5, relative to the preceding digits. As may readily be seen, detected change points were

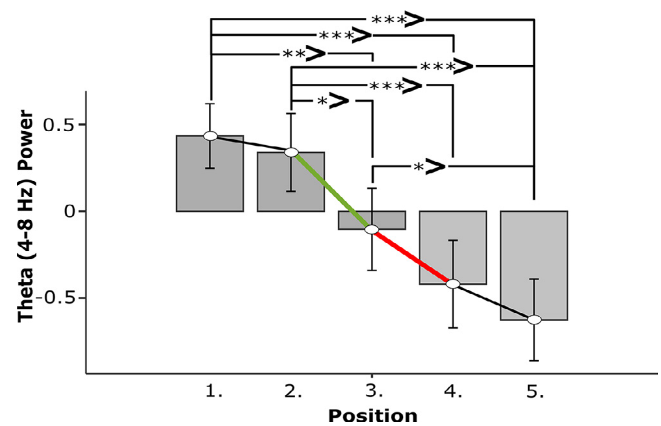

Fig. 4. The event-related theta (4-8 Hz) power values for each digit positions in the 5-ds backward task. The vertical axis shows the average theta power for each digit across subjects. The green (in 22 participants) and red (in 20 participants) lines represent where the theta power values changed most strongly among the four transitions between the five digits. The error bars on bar plots denote the standard error of the mean. Asterisks indicate statistical significance (*: $p \leq .05$, **: $p \leq .01$, ***: $p \leq .001$).

not uniformly distributed among the possible four transitions between the five digits ($X^2(3, N=42) = 42.19$, $p < 0.001$). In Fig. 4, the detected strongest changes between digits were demonstrated on the averaged data.

These findings showed where the greatest changes occurred, but we cannot know the direction of the changes from this analysis; the change could have happened in both directions. For investigating the direction of the power changes, we performed a repeated-measures ANOVA with the position factor. The results showed that position had a main effect on the theta power value of participants ($F(2.75, 112.61) = 14.2$, $MSe = 0.92$, $p < .001$, $\eta 2 = .07$). Pairwise comparisons revealed that participants had higher power for the first digit ($M = .43$, $SD = 1.20$) than third ($M = -.10$, $SD = 1.53$) (first vs. third, $t(164) = 3.10$, $p = .01$), fourth ($M = -.42$, $SD = 1.63$) (first vs. fourth, $t(164) = 4.91$, $p < .001$), and fifth ($M = -.63$, $SD = 1.53$) (first vs. fifth, $t(164) = 6.10$, $p < .001$) digits. Theta power values were also higher for the second digit ($M = .34$, $SD = 1.45$) than third (second vs. third, $t(164) = 2.55$, $p = .05$), fourth (second vs. fourth, $t(164) = 4.37$, $p < .001$) and fifth digits (second vs. fifth, $t(164) = 5.56$, $p < .001$). The third digit had higher power than the fifth digit ($t(164) = 3.01$, $p = .02$). There were no other differences between positions (*ps* $> .21$). In other words, there were significant decreases in power values after the second and third digits (Fig. 4, Fig 5B). Together with these results, we understand the changes that were depicted by the findchangepts algorithm had a decreasing pattern.

3.3. *EEG-behavior interaction Results*

Correlation analyses between behavioral data, namely, 5-ds recall scores, and EEG data were conducted with bivariate linear correlation (Pearson correlation, 2-tailed). As EEG data, delta and theta mean power values of each response to a set of digits were employed for the fronto-central and parieto-occipital regions, separately.

The subjects with increased fronto-central delta power during the item encoding had the higher recall scores ($r = 0.396$, $p = 0.019$) while no correlation was found between the parieto-occipital delta and recall scores ($r = 0.144$, $p = 0.411$) (Fig. 6A). There were no significant correlations between recall scores and theta responses in any locations as well (FC: $r = 0.096$, $p = 0.584$, PO: $r = -0.062$, $p = 0.722$) (Fig. 6B).

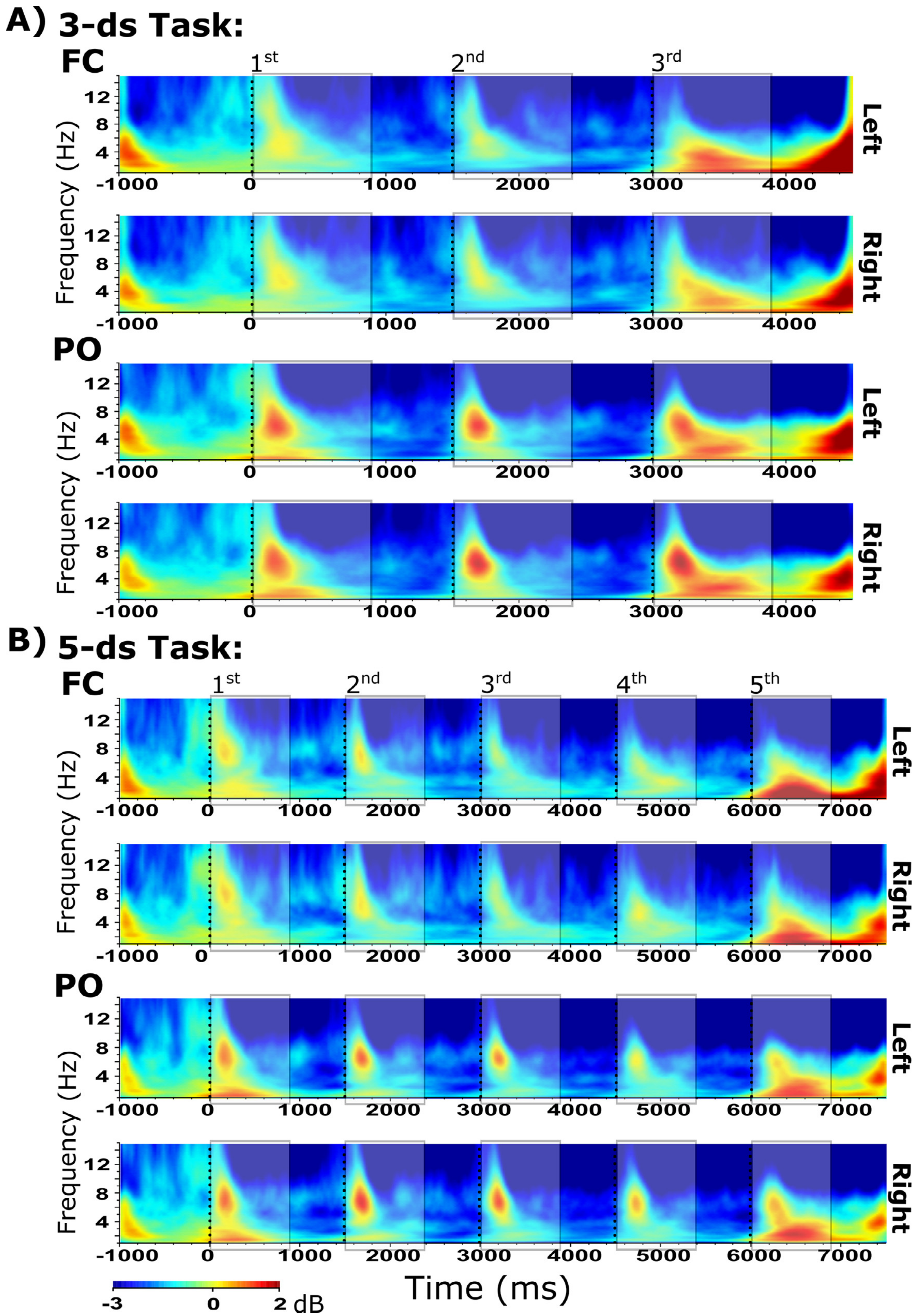

Fig. 5. The grand average figures of event-related power analysis (1-15 Hz) in the time-frequency domain during the digit span backward task. A) The grand average figures of event-related power analysis in the time-frequency domain in response to digits in the 3-ds backward task. The fronto-central area (upper) and parieto-occipital (bottom) areas for both hemispheres were presented in the figures. **B)** The grand average figures of event-related power analysis in the time-frequency domain in response to digits in the 5-ds backward task. The fronto-central area (upper) and parieto-occipital (bottom) areas for both hemispheres were presented in the figures. The X-axis represents time, and the Y-axis represents frequency; the point at which the first stimulus (digit) from the digit span set arrives is marked as a zero point on the X-axis. The point where each digit in a set comes from is indicated by black dashed vertical lines. And the 900 ms time interval that digits were presented in each set was marked with the gray transparent blocks on the plots. FC: fronto-central, PO: parieto-occipital, ds: digit span.

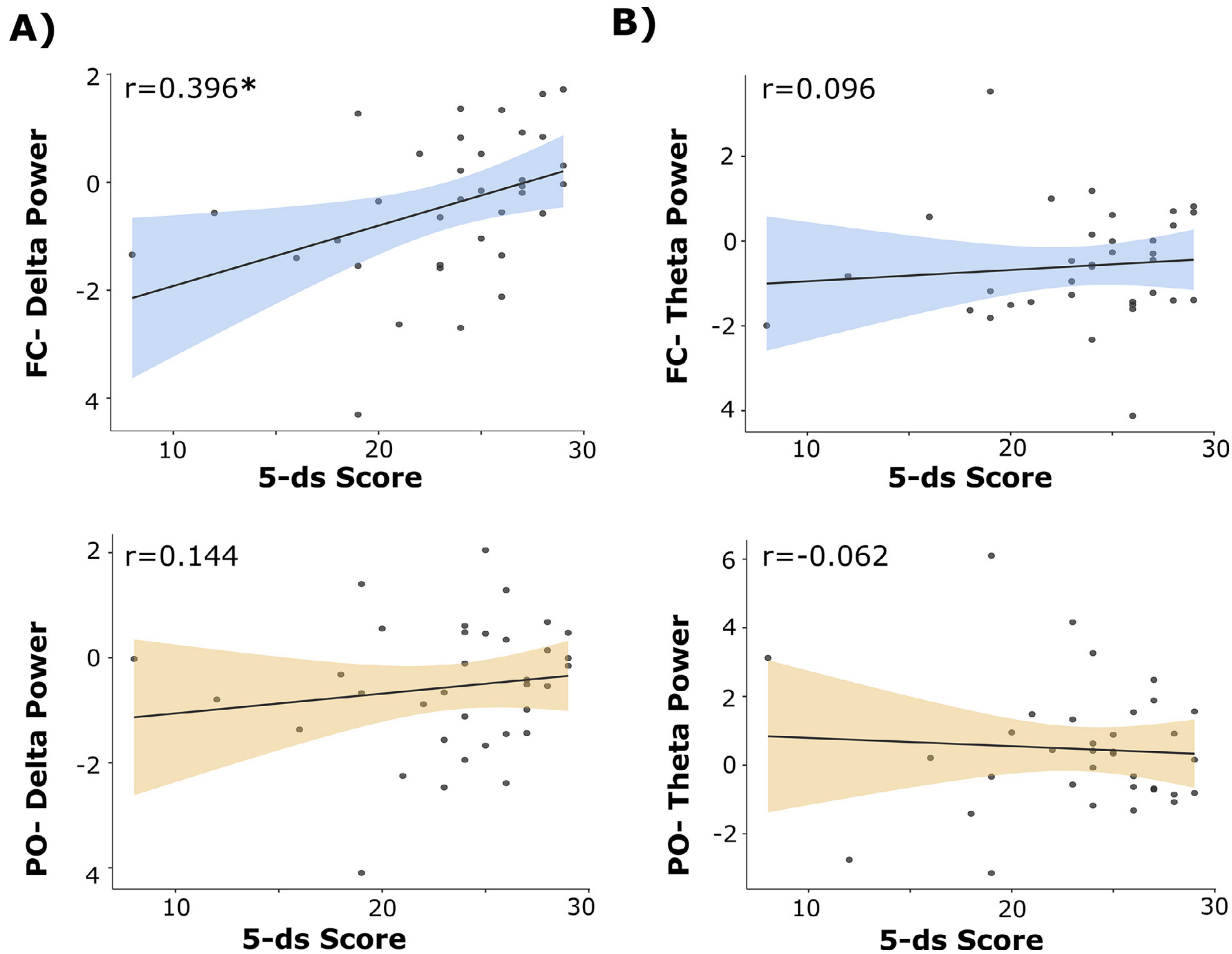

Fig. 6. The scatter plots of the correlation analysis result. A) The scatter plots of the correlation between the task scores and delta responses (1-3.5 Hz) in the FC (upper) and PO (bottom) areas. **B)** The scatter plots of the correlation between the task scores and theta responses (4-8 Hz) in the FC (upper) and PO (bottom) areas. FC: fronto-central, PO: parieto-occipital, ds: digit span. Asterisks indicate statistical significance ($p < 0.05$). The shaded area denotes the standard error. Dots represent the observed scores.

4. Discussion

Here we mainly aimed to investigate how brain theta and delta oscillations reflect the item position and number of items (to be held) during the encoding process in the working memory digit span backward task. Specifically, we searched for the "serial position" and "chunking" effects on delta and theta responses over the fronto-central and parieto-occipital areas. As an oscillatory reflection of the serial position effect, we expected increased delta power at the first and last digit compared to the middle digit(s). Our results demonstrate the delta responses were higher for the first and last items than for the middle items in the digit list, which match nicely the suggested "serial position curve" model (Murdock, 1962; Murre & Dros, 2015). Besides that, for theta frequency responses, as a sign of the chunking strategy, we expected altered oscillatory dynamics around the 3rd or 4th digit in light of our tendency to group items in three or four (Cowan, 2001, 2005, 2010). In line with the theories that emphasize memory chunks, change in the theta responses during the digit list encoding occurred during transitions to the third or fourth item; and the direction of change was downward, namely, theta responses to particularly the 3rd or 4th item decreased relative to preceding items. Furthermore, a positive correlation was found between frontal delta responses and task performance. This correlation was specific to location and frequency. Additionally, even though the primary aim of the current study was not to investigate number perception itself, the task used in the study naturally involved number processing as well. Therefore, according to previous literature on number processing studies (Hesse et al., 2017; Rinsveld et al., 2020), one might expect greater parieto-occipital (posterior) brain responses, and right hemisphere dominance, during number processing. Accordingly, results showed that the parieto-occipital areas had higher theta responses in the right hemisphere than the left, which supports previous studies (Hesse et al., 2017; Rinsveld et al., 2020) that showed the importance of the right parietal-occipital activation during number perception.

The serial position effect is a behavioral finding that experimental psychology studies on memory have widely demonstrated. Accordingly, the first (primacy effect) and last items (recency effect) in a list are recalled better than the middle ones. This is also called the serial position curve. This U-shaped curve shows the learning curve of the items in the list. Our study showed that delta oscillations reflect the suggested serial position effect with a higher delta power in response to the first and last items than the middle during the item list encoding. The most accepted model of the mechanism underlying the serial position effect is the dual-store processing model (Atkinson & Shiffrin, 1968; Talmi et al., 2005). In this model, the serial position effect relies on a distinction between short-term memory and long-term memory (Glanzer & Cunitz, 1966; Waugh & Norman, 1965). And per the concept, serial position effect occurs because the initial items on a list are retrieved from long-term memory, since the earliest items are rehearsed the most, thereby reinforcing their place in memory. The last items on the list, on the other hand, are still in short-term memory and hence can be retrieved without rehearsing. Atkinson, & Shiffrin (1968) suggest that the primacy effect in this model is also strictly related to the number of items in the list. Accordingly, if the list exceeds the "rehearsal buffer" then the presentation of new items forces a move of older items into long-term memory (Lehman & Malmberg, 2013). Another explanation of the serial position effect is based on attentional processes (Azizian & Polich, 2007; Melton, 1963; Page & Norris, 1998; Sederberg et al., 2006). In the scope of this claim, people may pay greater attention to the first and last items in the list, which creates "anchor points" for better learning the rest of the information by reducing the demands on memory. And in our case, considering the serial position effect was seen in the delta responses even for the 3-ds task, which is within the suggested memory limits in terms of the number of items to be held, possibly not only dual-store mechanisms but also attention allocation mechanisms might be involved. Therefore, it can be thought that the serial position effect reflected by delta oscillations is more related to immediate memory and attention-related processes, which these roles of the delta have been shown in many previous studies (Başar-Eroglu et al., 1992; Ergen et al., 2008; Harper et al., 2017; Polich & Kok, 1995; Sutton et al., 1965). In addition to this "serial position curve" reflected in delta, the last digit had a higher delta response than the first digit, especially for the FC location. It may indicate that participants are aware, either consciously or unconsciously, that the task list (digit set) has ended, allowing the required brain processes to prepare for recalling the digits backward. This additional process that is not present in the other digit positions (knowing that the recall process will start right after it) may have caused the greater delta response for the last digit due to the load it created. This is also in line with Wilsch & Obleser's (2006) findings that show higher delta may be related to the stimuli encoding and subsequent reduction of memory load (Wilsch & Obleser, 2016). Overall, it seems, here, delta responses serve as the neural start and end markers of the encoding of a list.

According to Cowan (2001; 2005; 2010), the limit of the mental storage capacity is 3-4 (up to 5). Therefore, it is assumed that the created chunks consist of grouping 3-4 items. Additionally, Nogueira et al. (2015) showed increased late positive slow waves during encoding the successively presented words when the items were chunked compared to the control condition. Accordingly, we hypothesized that created chunks in mentioned strategy may be reflected by theta oscillations since theta is majorly associated with the item encoding in literature. And as we expected, in line with Cowan's suggested mental storage capacity (3-4 items) and Nogueira et al. (2015)'s ERP study, event-related theta oscillations showed a decreasing pattern starting with the 3rd or 4th item. Similarly, Agam & Sekuler (2007) showed that EEG response declined as more chunks had to be stored, and they discussed it as the "interactions between working memory and visual perception" (Agam & Sekuler, 2007). They suggested memory load influences how the brain reacts to visual inputs. Azizian & Polich (2007) also found decreased EEG responses with the incoming stimulus in the encoding task as well, however, they associated the pattern found in EEG mostly with a decrease in attention with the approaching stimuli. According to them, the reason for the decrease in the EEG response to incoming stimulus was that each successive stimulus receives less attention than the previous one (Brown et al., 2000; Page & Norris, 1998). As a matter of fact, these two discussion points, namely, mental storage capacity limit and attentional decrease, also cannot be considered as purely separate processes. Considering capacity-limited attentional processes (Marois & Ivanoff, 2005) it is inevitable that exceeding this limit will lead to the creation of a way to better encoding, such as memory chunks. Therefore, it is very likely that these two bottlenecks (capacity-limited attentional processes and object encoding limit) are already interacting with each other and, accordingly, have led to the development of strategies. And yet, both limitations might be responsible for the created memory chunks during the item list encoding, which is reflected by the theta oscillations. Here we should also note that our results indicated that created chunks consist of 2 or 3 items, which is 1 item below the suggested memory limit (3 or 4). There may be two possible reasons why the chunks found here contain fewer items (2 or 3) than the suggested capacity limit (3 or 4): I) The total number of items was already low (5 digits were presented in a set), which may have caused the chunks to consist of fewer items. II) To optimize performance, it might have been more strategic to make smaller chunks because of the additional cognitive load as participants had to remember the sequences in "reverse" order for the digit span "backward" task.

Based on the studies in which increased slow oscillatory (< ~8 Hz) responses for the successfully encoded items in the anterior areas were shown (De Vries et al., 2018; Sederberg et al., 2006; Summerfield & Mangels, 2005; Weiss & Rappelsberger, 2000), accordingly, we expected a positive correlation between task scores and anterior EEG responses. Our results indicate that the anterior delta, but not theta, may relate to successful subsequent recall performance. However, in the literature, the most pronounced frequency that reflects the subsequent memory is theta oscillations, contrary to our findings (Friese et al., 2013; Herweg et al., 2020; Klimesch et al., 2004; Köster et al., 2018; Solomon et al., 2019; Staudigl & Hanslmayr, 2013). There are few studies in which similar subsequent memory effects have been shown for delta frequency (Sederberg et al., 2006; Weiss & Rappelsberger, 2000). According to these studies, delta power as response to the presented stimuli (visually and/or auditorily presented words) was higher for later successful recall. This frequency specific subsequent memory effect found in our study for delta frequency, but not for theta, might be specific to the task used in our study (digit-span backward), considering that most of the studies in the literature showing theta subsequent memory effect used the object (pictural) encoding tasks mostly.

All in all, the results of this study may suggest that different frequencies might be responsible for different elements of serial encoding that have previously been demonstrated mostly in behavioral studies. For further research, our findings on EEG indicators of the memory processes could provide a deeper insight which may also lead to more goal-directed neuromodulation approaches, especially for the clinical populations who have difficulties in these memory processes and encoding strategies.

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Data and Code Availability

The data that support the findings of this study are available from the corresponding authors on reasonable request. In this study all participants have signed an informed consent form approved by the local ethic committee stating that their data will only be made accessible to a third person for the purpose of scientific research. There was no novel code written to generate the findings. The data acquisition, processing, and analysis was performed using publicly available software and/or functions as described in "Methods" section.

Declaration of Competing Interest

None.

Credit authorship contribution statement

Tuba Aktürk: Conceptualization, Investigation, Project administration, Formal analysis, Software, Visualization, Writing – original draft, Writing – review & editing. **Tom A. de Graaf:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Furkan Erdal:** Conceptualization, Visualization, Writing – original draft. **Alexander T.**

Sack: Conceptualization, Supervision, Writing – review & editing. **Bahar Güntekin:** Conceptualization, Methodology, Resources, Supervision, Writing – review & editing.

Data Availability

Data will be made available on request.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2022.119650.

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