Endogenous Theta as a Function of Task Load and Working Memory Capacity: Revisiting the Role of Slower Frequencies in Theta–Gamma Coupling

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Abstract

■ Recent findings have shown the influential role of theta–gamma cross-frequency coupling in the maintenance of items in working memory (WM). Specifically, it has been proposed that individual items are represented within gamma oscillations that are nested within slower theta waves. Thus, longer theta cycles would theoretically allow the retention of more items. On the basis of this theory, the present preregistered study aimed to test whether slowing theta rhythms via 4 Hz of transcranial alternating current stimulation over the frontoparietal network improves WM capacity. Given the potential role of individual differences in stimulation effects, participants were divided into high and low WM capacity groups based on initial screening. In addition, task difficult was also manipulated to maximize the likelihood of obtaining an improvement in performance. Contrary to our hypothesis, transcranial alternating current stimulation did not improve behavioral outcomes regardless of task difficulty or baseline WM capacity. Poststimulation EEG effects were also analyzed, but no modulation of theta power, peaks, or phase synchronization was found. Importantly, differences in mean theta frequency were observed before any stimulation between high- and low-capacity WM participants, with higher frequencies present in participants with better WM performance. Furthermore, higher mean frequency was also observed in high-load trials versus low-load trials. These findings contradict the predictions of the theta–gamma coupling theory. Taken together, these results raise questions about the validity of the theta–gamma coupling theory to explain cortical dynamics related to WM. ■

INTRODUCTION

Working memory (WM) can be defined as the capacity to hold and manipulate information to facilitate goal-directed behavior. Previous research on its neural correlates has shown that WM entails the interaction of several brain regions, especially in frontoparietal cortex (Owen, McMillan, Laird, & Bullmore, 2005). In this way, it has been proposed that neural oscillations (rhythmic patterns of electrical activity coming from the brain) could support WM by facilitating long-range connectivity between relevant brain areas (D'Esposito & Postle, 2015; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005; Buzsáki & Draguhn, 2004; Gazzaley, Rissman, & D'Esposito, 2004).

WM maintenance has been associated to neural oscillations in the theta (4–7 Hz) and gamma (40–70 Hz) frequency range (Sauseng, Peylo, Biel, Friedrich, & Romberg-Taylor, 2019; Miller, Lundqvist, & Bastos, 2018; Roux & Uhlhaas, 2014; Lisman & Jensen, 2013). The theta–gamma coupling theory (Lisman & Jensen, 2013; Jensen & Lisman, 1996) proposes that maintenance occurs by coupling slow and fast brain waves. According to this theory, fast oscillations represent individual items, whereas slow waves, such as theta waves, organize these fast oscillations by locking them to different phases of the theta cycle. Theta–gamma coupling has been observed in both the hippocampus (Chaieb et al., 2015; Axmacher et al., 2010) and cortical regions (Fernández, Pinal, Díaz, & Zurrón, 2021; Brooks et al., 2020; Köster, Friese, Schöne, Trujillo-Barreto, & Gruber, 2014; Holz, Glennon, Prendergast, & Sauseng, 2010; Canolty et al., 2006).

A clear prediction derived from the theta–gamma coupling theory is that lower frequency theta waves (i.e., longer theta cycles) allow a greater number of gamma bursts to be nested, thereby enabling more information to be retained in WM (Axmacher et al., 2010). This prediction can be tested by slowing down theta rhythms extrinsically and observing whether this increases WM capacity (WMC). One way to extrinsically modulate endogenous oscillations is using transcranial alternating current stimulation (tACS). tACS is a widely used noninvasive brain stimulation technique (Antal et al., 2008, 2022; Elyamany, Leicht, Herrmann, & Mulert, 2021; Fröhlich, Sellers, & Cordle, 2015; Helfrich et al., 2014) that applies weak electrical currents (typically sinusoidal) to the scalp using two or more electrodes, simulating natural

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brain oscillations. Part of this current reaches cortex by traveling through the skull, allowing the entrainment of distant brain regions to the stimulation frequency, which can improve or hinder connectivity between these areas (Alekseichuk et al., 2019; Schwab, Misselhorn, & Engel, 2019; Weinrich et al., 2017).

Several studies have applied theta tACS (3–7 Hz) to synchronize theta endogenous oscillations between regions of the frontoparietal network with the aim of improving WM functioning (Biel, Sterner, Röll, & Sauseng, 2022; Jones, Arciniega, & Berryhill, 2019; Reinhart & Nguyen, 2019; Pahor & Jaušovec, 2018; Tseng, Iu, & Juan, 2018; Kleinert, Szymanski, & Müller, 2017; Violante et al., 2017; Polanía, Nitsche, Korman, Batsikadze, & Paulus, 2012). The frontoparietal network is typically targeted because it plays a central role in WM functioning (D'Esposito & Postle, 2015; Owen et al., 2005). Specifically, left dorsolateral prefrontal cortex (DLPFC; F3 position) and left posterior parietal cortex (PPC; P3 position) have been repeatedly associated with manipulation and maintenance of information in verbal WM (Barbey, Koenigs, & Grafman, 2013; Veltman, Rombouts, & Dolan, 2003; Wager & Smith, 2003). Moreover, both functional neuroimaging and electrophysiological studies have shown strong frontoparietal theta synchronization during verbal WM tasks, which has been interpreted as the top–down control from prefrontal regions over parietal ones (Roux & Uhlhaas, 2014; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010).

Polanía and colleagues (2012) were the first to apply theta tACS in phase (0° lag) between left DLPFC and left PPC (F3 and P3 positions, respectively), observing better performance in a verbal Sternberg task under a 6-Hz stimulation. However, subsequent studies have only partly replicated these seminal results (Pahor & Jaušovec, 2018; Kleinert et al., 2017; Violante et al., 2017). Biel and colleagues (2022) proposed that one reason for the inconsistency of results could be the way in which stimulation electrodes were referenced. Thus, building upon Polanía and colleagues (2012), they used a similar frontoparietal montage (F3–P3 positions) but implementing a ring configuration to improve current focality (Alekseichuk et al., 2019; Saturnino, Madsen, Siebner, & Thielscher, 2017; Bortoletto, Rodella, Salvador, Miranda, & Miniussi, 2016). They observed enhanced WM performance when in-phase theta stimulation was applied online—that is, concurrently with the task—but only when participants completed a more demanding task than that used by Polanía and colleagues (2012). Therefore, these findings suggest that both electrode placement and task difficulty appear to be crucial factors for observing stimulation benefits (Bender, Romei, & Sauseng, 2019; Violante et al., 2017; Hoy et al., 2015; Jaušovec, Jaušovec, & Pahor, 2014; but see Wu et al., 2014).

A second factor that has been reported to determine WM performance benefits due to stimulation is individual differences in WMC. Several studies have shown that low performers may benefit the most of noninvasive brain stimulation for enhancing WM (e.g. Sahu & Tseng, 2021; Arciniega, Gözenman, Jones, Stephens, & Berryhill, 2018; Tseng et al., 2018; Feurra, Galli, Pavone, Rossi, & Rossi, 2016; but see Hsu, Juan, & Tseng, 2016, for the opposite pattern) because they have greater room for improvement. Despite the apparent importance of these factors—task difficulty and individual differences in baseline WMC, no study has systematically modulated both when applying tACS.

Among the studies attempting to synchronize different brain regions using theta tACS, only two have explored the EEG aftereffects of stimulation, but results were inconsistent. Pahor and Jaušovec (2018) observed an unexpected theta amplitude reduction compared with sham. On the other hand, Kleinert and colleagues (2017) observed a peak power modulation in alpha, which was not specific to the stimulated frequency band. Besides, none of them tested the changes in synchronization between the stimulation electrodes.

Another group of studies that successfully modulated WM performance using tACS did not focus on synchronizing different regions. Instead, they closely followed the previously mentioned rationale of Lisman's theory—entraining at slower frequencies to slow down endogenous oscillations and thereby increase the number of gamma cycles nested within each theta cycle (Aktürk, de Graaf, Güntekin, Hanoğlu, & Sack, 2022; Guo, Li, Zhang, & Liu, 2021; Bender et al., 2019; Pahor & Jaušovec, 2018; Wolinski, Cooper, Sauseng, & Romei, 2018; Alekseichuk, Turi, de Lara, Antal, & Paulus, 2016; but see Vosskuhl, Huster, & Herrmann, 2015; Jaušovec et al., 2014). Contrary to Polanía and colleagues (2012), these studies typically used visuospatial WM tasks and applied slow a 4-Hz theta—or individualized frequencies—tACS to different cortical regions. To our knowledge, only two studies explored the EEG aftereffects of theta tACS (Aktürk et al., 2022; Vosskuhl et al., 2015). Aktürk and colleagues (2022) found that tACS at individualized theta frequencies minus 1 Hz led to improved memory performance and increased frontoparietal theta connectivity, and Vosskuhl and colleagues (2015) reported an amplitude increase at ~6.7 Hz after applying 4 Hz of stimulation. However, none of them measured the specific aftereffects that should be derived from the theory, for example, slowing of mean theta frequency after stimulation. Furthermore, no study has tested whether theta is modulated differently in participants with higher or lower WMC, or when more or less information should be maintained, as the theory would predict.

In the present preregistered study, we aimed to integrate these two strategies from previous studies: synchronizing frontoparietal regions at the theta frequency specifically at a slow 4 Hz rhythm, as the theta–gamma coupling theory proposes that slower frequencies facilitate the maintenance of more information in WM. For that, an online 4-Hz tACS over F3 and P3 was applied. Online stimulation (i.e., concurrent with the task) was selected to target the active oscillations during WM maintenance. Unlike offline stimulation, online stimulation allows for the evaluation of the interactions between endogenous and exogenous rhythms during cognitive processing (Biel et al., 2022; Polanía et al., 2012). On the basis of previous findings, we considered both task difficulty (Biel et al., 2022) and interindividual differences in WMC (Krause & Cohen Kadosh, 2014) as potential moderators. In addition to behavioral outcomes, we investigated the effects of tACS on EEG both during the task and at rest. Thus, the present work has two main objectives: (i) to assess whether slowing down theta rhythms in the frontoparietal network via a 4-Hz tACS would improve WM performance and (ii) to evaluate how baseline WMC and task difficulty modulate the effects of theta tACS on WM performance. We hypothesized that participants with lower WMC would benefit more from a 4-Hz theta tACS, particularly during high-load task conditions. In addition, we predicted that the EEG aftereffects of stimulation would show a reduction in the predominant theta frequency and an increase in the target theta power frequency—this effect being more prominent in participants with lower WMC and when more information needs to be maintained.

METHODS

Participants

To identify participants with high and low WMC, 352 undergraduate students from the University of Murcia were screened in exchange for course credit. On the basis of their performance, 220 students were selected, 99 assigned to the high WMC group and 121 assigned to the low WMC group (see below for details on the screening task and classification procedure). These participants were invited to the laboratory, and 108 ultimately took part in the experimental session after applying exclusion criteria. The exclusion criteria were pregnancy, personal or close family history of neurological or psychiatric disorders, metal implants, migraines, epilepsy, cardiac pacemaker, or infusion pumps. After rejecting data from 11 participants due to device issues, the final sample was 97 participants: 49 high WMC (36 female; $M_{\text{age}} = 19.82$ years, $SD_{\text{age}} = 4.12$; $M_{\text{span}} = 6.80$) and 48 low WMC (42 female, $M_{\text{age}} = 19.48$ years, $SD_{\text{age}} = 1.22$; $M_{\text{span}} = 4.75$).

The sample size for the tACS session was previously determined using G*Power 3.1 software to detect a medium effect size ($\eta_p^2 = .06$) with an alpha level set at .05 for the most stringent interaction term of the design to obtain .80 power. A minimum sample size of 92 participants was required; thus, a sufficient sample was obtained. All participants indicated that they had normal or corrected vision.

Approval for this study was obtained from the ethics committee at the University of Murcia, and the research was conducted according to the ethical standards of the 1964 Declaration of Helsinki.

Tasks and Stimuli

Screening (Session 1)

Participants completed a digit span task programmed using JavaScript, HTML, and CSS on their personal mobile phones. Although the task was performed individually, participants completed it in groups of up to 30 people, under the supervision of a researcher. The task consisted of 15 trials. Each trial began with the presentation of a digit sequence displayed at the center of the screen at a rate of one digit per second (800 msec on, 200 msec off). After the sequence, nine buttons displaying the digits 1–9 appeared in a 3 × 3 grid. Participants used these buttons to reproduce the sequence in the exact order of presentation. As they responded, their input was shown on the screen. A "#" button was available to mark forgotten digits, a backspace button allowed correction of the last entry, and a "Next" button enabled participants to submit their response and proceed to the next trial. The 15 test sequences included three lists of each length, ranging from four to eight digits. Before the main task, two 3-digit practice trials were presented to familiarize participants with the procedure. Digit sequences were randomly generated with the following constraints: All digits within a list were unique, consecutive numbers (e.g., 3–4) were not allowed, arithmetic progressions of three elements (e.g., 2–4–6) were avoided, the same digit could not appear in the same position in two consecutive trials, pairs of consecutive digits from one list could not be repeated in the next, and the last digit of a list could not be the first digit of the following one.

Three measurements could be obtained from this task: the total number of digits correctly recalled (correct item and correct serial position; maximum = 90), the number of complete lists correctly recalled (maximum = 15), and the participant's span (defined as the longest list length for which the participant correctly recalled at least two lists). The criteria to classify participants in the low, intermediate, or high WMC groups were as follows. Participants were classified as low WMC if they correctly recalled less than 70 digits, correctly recalled less than eight lists, and had a digit span lower than six. Participants were classified as high WMC if they recalled 75 or more digits, recalled nine or more complete lists, and had a span of six or more. The rest of the participants were classified as intermediate and were not invited to participate in the stimulation experimental session. By this procedure, 34.38% of the participants were classified as low and that of 28.13% as high in capacity.

Main Task (Session 2)

In the tACS session, participants performed a modified version of the delayed letter discrimination task used by Polanía and colleagues (2012). In Figure 1, there is a schematic representation of the WM task used in the experiment. Each trial began with a fixation point (+) for 1000 msec followed by the sequential presentation of

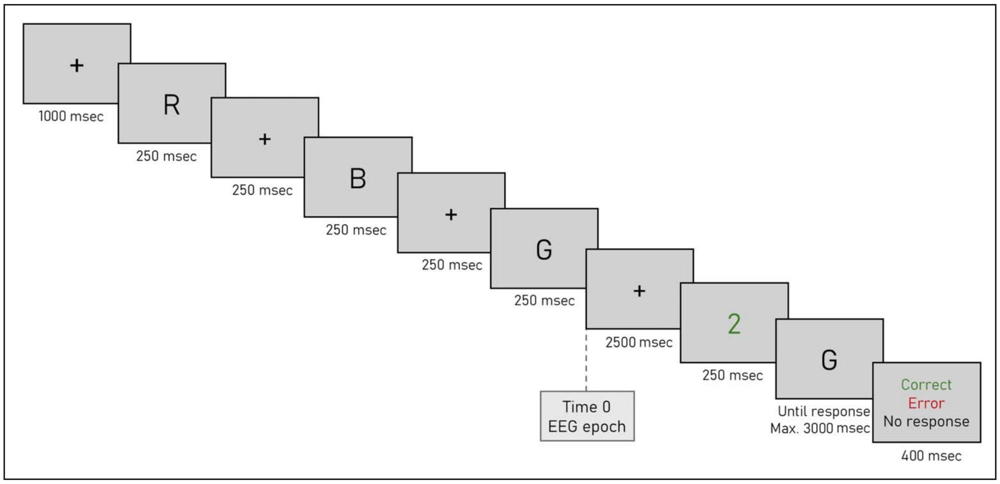

Figure 1. Schematic synthesis of a Load 3 trial from the delayed letter discrimination task used during the stimulation session.

three or five (low- or high-load trials, respectively) capital letters. Each letter had a duration of 250 msec followed by a fixation cross for another 250 msec. After the last letter, another fixation point was presented for 2500 msec (usually referred to as "delay period"). Then, a number in green color was presented in the center of the screen for 250 msec. This number would be from one to three in the low-load trials and from one to five in the high-load trials, and it referred to the position that occupied one of the previously presented letters. Then, another capital letter was presented for a maximum time of 3000 msec and participants had to judge whether this letter corresponded to the position indicated by the green number. The probability of the letter being correct was 50%, and for the incorrect trials, a letter to be maintained in another position was displayed to avoid answering merely by familiarity. The button responses (i.e., right or left) were counterbalanced across participants. Then, a feedback display was presented for 400 msec followed by a 1000-msec blank screen that preceded the presentation of the next trial. The stimuli were randomly selected from a pool of 18 possible letters (B, C, D, F, G, H, J, K, L, M, P, Q, R, S, T, V, X, and Z). All letters had the same likelihood of being presented, and all of them were presented once before being repeated. Additionally, a letter would never repeat itself before the following 16 letters were presented.

The task was programmed with E-Prime 3 (Psychology Software Tools Inc., 2016), and responses were collected via a five-button Chronos device (Psychology Software Tools Inc., 2016). The task was performed in an individual sound-attenuated booth where participants were seated around 70 cm from the screen. Stimuli were presented on a 23-in. flatscreen LED monitor (LG 23MP68VQ-P) with 1920 × 1080 pixels on a gray background (red, green, blue 192,192,192).

Procedure

Participants classified as high or low WMC based on the screening results were contacted to attend the laboratory in a second session. Menstruating participants who were not using hormonal contraceptives were dated outside of days 13–15 of their menstrual cycle to avoid ovulatory days, which has been shown to influence the effects of brain stimulation (Rudroff, Workman, Fietsam, & Kamholz, 2020). It was calculated by asking about their last four periods to calculate the average of their cycle length and subtracting 14 days (average luteal phase duration). Then, this was added to the onset day of their last period. If the experiment date matched with this estimated ovulatory day, the day before or the day after, it was rescheduled to avoid ovulation.

Once they arrived at the laboratory for the main task, they were assigned to the active or sham stimulation group (between participants factor). To ensure balanced sample sizes, the assignment was carried out separately within each WMC group and alternated based on recruitment order. Thus, if the previous high WMC participant was assigned to the active group, the next one was assigned to the sham group). Both the participant and the experimenter were blinded both to the stimulation condition and to the WMC group the participant belonged to. Then, participants entered the individual isolated room, the transcranial electric stimulation (tES)/EEG electrodes were placed, and the task was explained to them. First, they remained with their eyes open and they completed 3 min of resting-state EEG recording. Then, the instructions for the memory task were displayed and they completed five practice trials of each type (i.e., low and high load). After practicing, they completed 30 randomly presented trials of each type while EEG was recording. Then, the message "PLEASE, CALL THE RESEARCHER" was displayed on the screen and the researcher would change from EEG to tACS. After that, they received either sham or active tACS while performing 120 randomly ordered trials, 60 low-load and 60 high-load trials. Following stimulation, the same message was displayed and the researcher changed again to EEG recording while the participants performed 60 more trials, 30 of each load condition. Then, the participants remained still with their eyes open to complete the last 3 min of resting-state recording

EEG. After finishing the experiment, they completed a survey about the stimulation sensations (Hemmerich, Lupiáñez, Luna, & Martín-Arévalo, 2023; Fertonani, Ferrari, & Miniussi, 2015).

tACS and EEG Protocol

tACS was administered with a StarStim 8 wireless system (Neuroelectrics) connected to hybrid tES/EEG NG Pistim circular electrodes (pi cm^2). Stimulation electrodes followed the 10–20 system and were located at the left DLPFC and left PPC, respectively, at the F3 and P3 positions. The stimulation was administered in phase, 0°, between the F3 and P3 electrodes, and return electrodes surrounding stimulation electrodes were located on positions F7, Fz, C3, P7, and Pz, in a triangular focal shape. Stimulation at F3 and P3 was set at 4 Hz with an intensity of 1500 μA, zero-to-peak, and return electrodes at 600 μA (following the montage from Biel et al., 2022). The duration of the stimulation was 15 min, with 1 min ramp-up and ramp-down and was administered online. The sham stimulation group received only the ramp-up and ramp-down, with no active stimulation during the remaining time. This was used to mimic the sensory experience of the active group without receiving actual stimulation.

EEG data were also collected using the Starstim 8 system. Apart from the stimulation electrodes, the additional Cz electrode was recorded. The reference electrode was placed on the right earlobe using an EarClip electrode. Data were recorded with a sampling frequency of 500 Hz, a bandwidth of 0–250 Hz. Electrode impedances were kept below 5 kΩ. EEG data were collected both during resting and while performing the task, before and after stimulation (see Figure 2). During resting-state recording, participants were instructed to remain with their eyes open looking at the fixation point in the center of the screen.

EEG Preprocessing and Analyses

Preprocessing was conducted in MATLAB using the EEGLAB toolbox v2024.1 (Delorme & Makeig, 2004). The raw data sets were imported to EEGLAB using the NE EEGLAB NIC plugin. EEG data were downsampled to 250 Hz, high pass filtered to 1 Hz, and low pass filtered to 120 Hz using *pop_eegfiltnew*. Then, the *pop_cleanline* function was used to clean the 50 line noise and the 100 Hz harmonic, and data were rereferenced to the average of all the electrodes. Afterward, the resting epochs were extracted, as well as the delay epochs. The delay epoch was from 0 msec to 2499 msec, locked to the beginning of the delay after the last presented letter. The baseline correction used was the central 700 msec of the initial 1-sec fixation cross before the trial onset. Thus, the baseline duration time was equal in length across conditions, but occurred closer in time to the maintenance delay in the low-load trials (three letters between the baseline

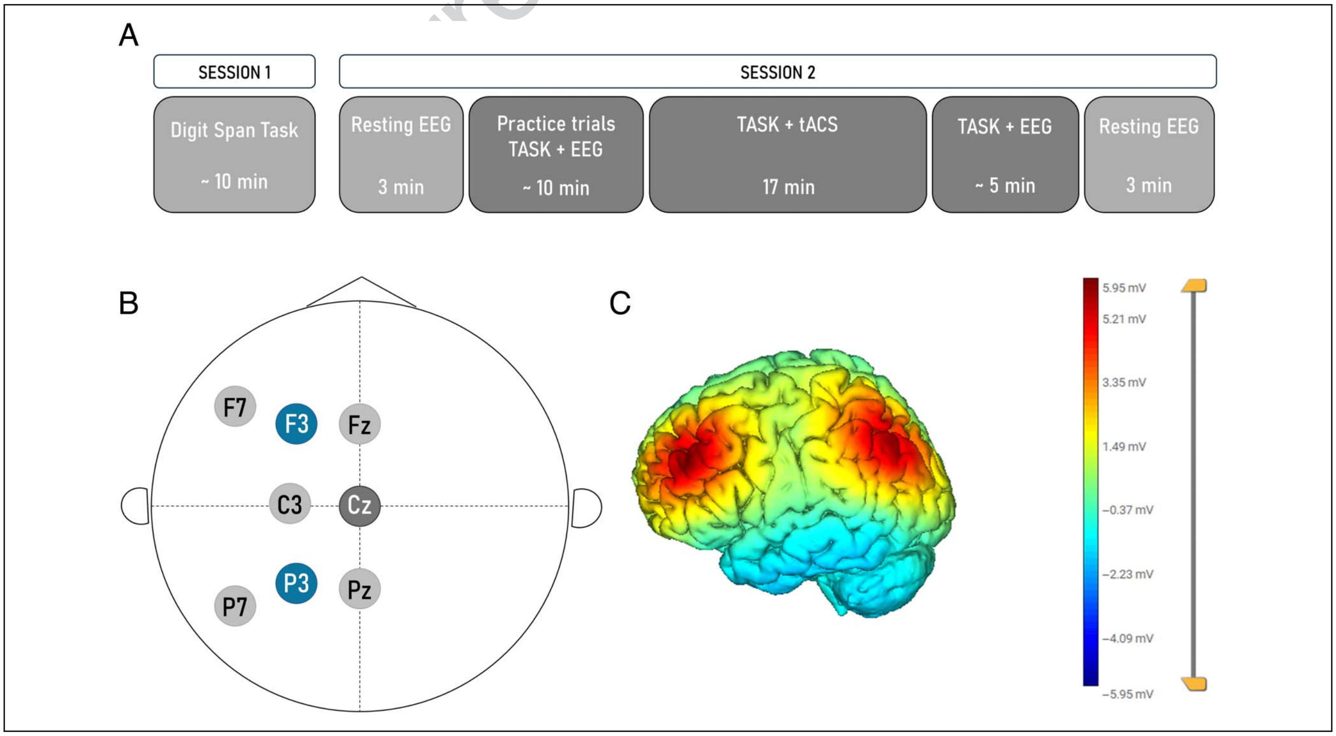

Figure 2. (A) Experimental procedure of the two sessions. (B) Stimulation montage, where blue electrodes represent the active stimulation electrodes, light gray electrodes represent reference electrodes, and the dark gray electrode is only used for EEG recording. (C) Electric field.

period and the maintenance delay) than in the high-load trials (five letters between the baseline period and the maintenance delay). Consequently, the baseline periods spanned from −1950 to −1250 msec for the low-load trials and from −3000 to −2300 msec for the high-load trials, relative to the onset of the maintenance delay.[1] No baseline correction was applied to the resting-state epochs. Then, independent component analysis was run with the *pop_runica* function of EEGLAB. Artifacts were removed using the *pop_iclabel* function to classify the components. Then, those components classified with a probability higher than 0.7 as eye, heart activity, or channel noise, or higher than 0.5 as line noise, were flagged with the function *pop_icflag* and later removed from the data. Trials with no responses and errors were excluded from the EEG analyses.

Three main types of analyses were performed on the EEG data: power variations, theta band average and peak modulations, and phase synchronization of the stimulation electrodes. The phase synchronization analysis was not preregistered.

First, the power spectrum was calculated in resting and during the first and last block of the task (i.e., before and after stimulation). Analyses were performed with custom code using the fast Fourier transform (FFT) following the recommendations of Cohen (2014). Resting-state data were segmented into 2-sec epochs. The frequencies to calculate the FFT were determined with the function *linspace* with the maximum frequency in the Nyquist number (125 Hz), and the number was the half of the number of time points in an epoch plus one. A Hanning window was applied to each epoch. To determine the effects of stimulation in the power spectrum, the normalized percentage change was calculated for the EEG signal after stimulation/sham compared with the baseline (i.e., resting state or task signal average before receiving tACS). This normalization has several advantages over nonnormalized data, such as making the data more easily interpretable, standardizing it, and reducing differences that could be due to interindividual factors at baseline (Clayton, Yeung, & Cohen Kadosh, 2019; Cohen, 2014). Where X is the mean individual power spectrum, the percentage change formula was as follows:

$$\text{Percent change} = \frac{\left(X_{\text{post}} - X_{\text{pre}}\right)}{X_{\text{pre}}} \times 100 \qquad (1)$$

Before calculating the subsequent metrics, the aperiodic ($1/f$) component was subtracted from the power spectrum to obtain a clearer measure of the oscillatory peaks (see Supplemental Figure S3 for a visualization of the spectrum after the aperiodic correction). Subsequently, to obtain an estimate of the mean theta frequency for each participant and condition, the "gravity frequency" (gF), or weighted mean of the band (Hooper, 2005; Klimesch, 1997, 1999), was calculated. This is obtained as the weighted sum of the spectral frequencies of interest, divided by the total theta power:

$$gF = \frac{\sum (a(f) \times f)}{\sum a(f)} \qquad (2)$$

Where $a(f)$ is the power spectral at frequency f. In this case, the frequencies of interest were fixed in 3–7 Hz for all participants (i.e., theta band) and they were obtained in MATLAB in linear steps with the function *linspace* from 0 to Nyquist (i.e., 125) in $N/2 + 1$ steps, where N is the number of time points in the data delay. This returned 14 continuous frequencies for which power was obtained and z-normalized before calculating gF. Again, the percentage of change was calculated to allow the comparison of the two stimulation groups.

In addition, the peak theta frequency of each participant and condition was calculated. This analysis aimed to obtain the specific frequency with the maximum power in the theta band. To that end, spatio-spectral decomposition (SSD) was performed on the theta band of all concatenated data of each participant, regardless of the moment or stimulation condition. SSD maximizes the power at the peak frequency and reduces the noise of the neighboring frequencies, optimizing the signal-to-noise ratio of the frequency of interest and obtaining components with a "peaky" spectral profile (Nikulin, Nolte, & Curio, 2011). This allowed the extraction of the peak frequencies of 65 participants in resting and 57 on task. The peaks were obtained using the *findpeaks()* function from MATLABR2021b on the first component of the SSD FFT spectral data that showed a peak. If no peak was obtained, the data of this participant were not included in the present analysis. Then, the pre–post stimulation percentage change of the peaks was calculated for each participant and stimulation condition. Lastly, the functional connectivity between the two main stimulation electrodes (i.e., F3 and P3) was explored before and after stimulation to assess variations in long-range synchronization using a method called phase locking value (PLV; Lachaux, Rodriguez, Martinerie, & Varela, 1999). To calculate the PLV, the phases of the individual electrodes within the narrow band of interest (in this case, the theta band from 3 to 7 Hz) were first extracted via Hilbert transform, and the difference between these instantaneous phases was then computed. The PLV takes values ranging from 0 to 1, where a value of 0 indicates unsynchronized phases, and 1 indicates perfect phase synchronization. Similarly, an increase in the PLV value indicates an increase in synchronization between the two electrodes. The interest of this analysis was to determine whether connectivity between these two electrodes increased after stimulation. Again, to compare theta and sham stimulation groups independently of individual baseline synchronization, the percentage change of both groups was calculated in the same manner as for power spectrum.

Statistical Analyses

Behavioral data were preprocessed in RStudio (RStudio Team, 2022) and analyzed with JASP 0.19.0.0 (JASP Team, 2022). A significant level of $\alpha = .05$ was adopted. Post hoc tests were performed to explore the significant interactions. Holm–Bonferroni correction was applied to correct for multiple comparisons. Besides, for all analyses, if Mauchly's sphericity test reached statistical significance, Greenhouse–Geisser correction was applied. First, it was tested whether stimulation affected performance on the delayed letter discrimination task, depending on baseline WMC and task difficulty. As preregistered, two ANOVAs were performed on RTs and Accuracy (ACC) as dependent variables. Additionally, two additional exploratory ANOVAs were performed on discriminability (d') and Cowan's K value (Rouder et al., 2008; Cowan, 2001) to evaluate task performance. The d' metric was used to assess the participants' sensitivity to distinguish between target and nontarget stimuli independent of response bias. It is calculated as $d' = Z(H) - Z(FA)$, where H and FA are the hits and false alarms, respectively, and Z represents the z-score transformation of the probabilities. On the other hand, Cowan K is a measure used to calculate the estimated number of items that participants maintained in WM (i.e., storage capacity). Cowan's K formula is $K = (H - FA) \times N$, where K is the number of items remembered, H and FA are the hits and false alarms rates, and N is the number of items presented to be remembered.

The mean theta power, the mean theta frequency, and the PLV were used as dependent variables in the EEG analyses. The analyses were performed with WMC Groups (high and low) and Stimulation (4 Hz and sham) as between-participant factors and Task Load (low and high load) as within-participant factors. The moment of recording (pre–post) was also introduced in some analyses (specified in the Results section) as within-participant factors.

RESULTS

tACS Sensations

First, we evaluated whether participants that received theta stimulation reported a higher overall intensity of sensations than those in the sham group. To do this, we conducted an ANOVA with Stimulation Group as the factor and total sensation score (sum of all items) from the administered scale as the dependent variable. The results showed no significant differences in sensations between the two groups, $F(1, 95) = 2.696, p = .104, \eta_p^2 = .028$.

To further explore differences in specific sensations, we conducted independent one-way ANOVAs for each of the seven items on the scale (itching, pain, burning, heat, pinching, iron taste, and fatigue). p Values were corrected using the Holm–Bonferroni method to account for multiple comparisons. Results revealed no significant differences ($p > .05$) between stimulation groups for any individual sensation (see Supplemental Figure S1 and Table S1). Only when no correction was applied were significant differences observed in burning sensation, $F(1, 95) = 4.907, p = .029, \eta_p^2 = .049$, which was stronger in participants in the theta stimulation group ($M_{\text{theta}} = 0.63$, $M_{\text{sham}} = 0.33$, out of 4 points).

In addition, we performed another ANOVA using data from a specific question on the scale. In this question, participants had to guess whether they were receiving active stimulation or placebo, with responses options including "real," "placebo," or "I don't know." The frequency of each response type was compared between the theta and sham stimulation groups. This analysis also revealed no significant differences between the stimulation groups, $F(1, 95) = 0.318, p = .574, \eta_p^2 = .003$.

tACS Effects on WM Performance

To evaluate the effects of stimulation on task performance, analyses were performed separately during the task and pre–post stimulation. On RTs during stimulation, results from the main effect of Task Load (i.e., difficulty) were statistically significant, $F(1, 93) = 178.957, p < .001, \eta_p^2 = .658$, with faster RTs in the low-load condition ($M_{\text{low}} = 948$ msec, $M_{\text{high}} = 1106$ msec). The interaction WM Group × Load was also significant, $F(1, 93) = 5.092, p = .026, \eta_p^2 = .052$ (see Figure 3), with slower RTs in the high WMC group compared with the low WMC group when the load was high, although these post hoc differences did not reach statistical significance.[2] Importantly, no main effect or interaction involving Stimulation reached significance (all $ps \geq .153$). When the analysis was performed to compare the blocks before and after stimulation, no effect of Stimulation was observed in RTs. Only the main effects of Load (i.e., better performance in the low-load condition), $F(1, 93) = 187.253, p < .001, \eta_p^2 = .668$; Moment (i.e., better overall performance in the last task block), $F(1, 93) = 174.079, p < .001, \eta_p^2 = .652$; and the interaction WM Group × Load, $F(1, 93) = 11.476, p = .001, \eta_p^2 = .110$, showed statistical significant differences.

ACC analyses showed similar results. During stimulation, a significant WMC × Load interaction reached statistical significance, $F(1, 93) = 19.319, p < .001, \eta_p^2 = .172$, with more pronounced differences between both WMC groups in the high-load task condition (see Figure 3). These results show that the WMC groups and the task difficulty manipulations worked as intended because, overall, (1) the high WMC group performed better than the low WMC group at both high- and low-load conditions, $F(1, 93) = 22.439, p < .001, \eta_p^2 = .194$, and (2) accuracy was higher in the low-load than the high-load condition, $F(1, 93) = 282.201, p < .001, \eta_p^2 = .752$.

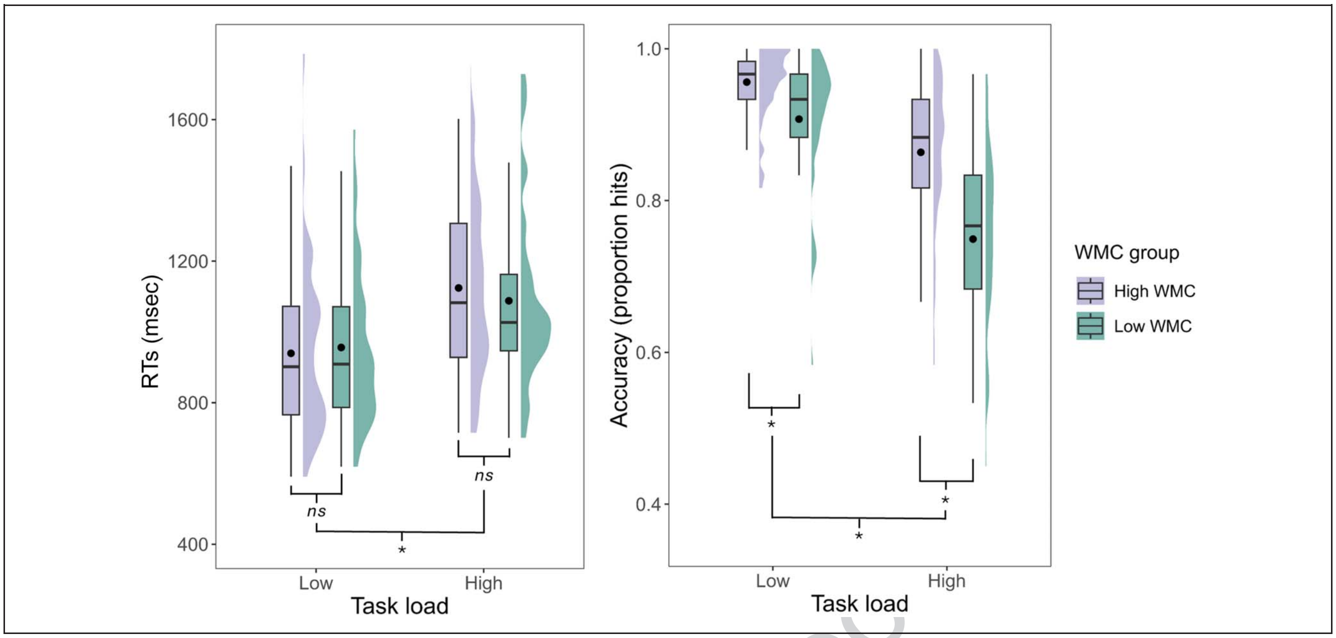

Figure 3. Working memory capacity Group × Task Load interaction in (A) RT and (B) accuracy. In the box plots, the central line represents the median, whereas the black point indicates the mean. The lower and upper limits of the box plot represents the first and third quartiles, respectively. Error bars represent the standard error of the mean.

The WMC × Task Load interaction was also observed when the ACC analyses were performed in the pre- and poststimulation blocks, $F(1, 93) = 37.240$, $p < .001$, $\eta_p^2 = .286$. In addition, the main effect of the Moment was significant, $F(1, 93) = 19.828$, $p < .001$, $\eta_p^2 = .176$, showing an overall improvement in the task with practice ($M_{\text{pre}} = 0.83$, $M_{\text{post}} = 0.87$). Importantly, no main effects or interactions with Stimulation were significant (all ps ≥ .161; $M_{\text{stim}} = 0.87$, $M_{\text{sham}} = 0.87$). Not finding significant results of stimulation due to a ceiling effect was discarded considering that the average accuracy in the high-load condition by the low WMC group (i.e., where effects were expected) was 0.75 (see Figure 4).

Although it was not preregistered, the same analyses were also performed on d' and K as dependent variables. Both analyses showed no significant main effect or interaction of Stimulation (all ps ≥ .153). And, again, significant WMC × Load interactions were observed on d' and K, with better performance in the case of the high WMC group in the more demanding condition, compared with the low WMC group. On d', this interaction was only observed on the blocks pre- and poststimulation, $F(1, 93) = 18.615$, $p < .001$, $\eta_p^2 = .167$, whereas it was significant both pre–post, $F(1, 93) = 26.050$, $p < .001$, $\eta_p^2 = .379$, and during stimulation, $F(1, 93) = 25.898$, $p < .001$, $\eta_p^2 = .218$, in K.

Overall, the results indicate that WMC groups differed, with the low WMC group consistently showing worst performance in all measurements. However, contrary to our hypothesis, Stimulation had no effect in either WMC group.

tACS Effects on Theta Power

Despite the absence of any behavioral effects, the impact of stimulation on brain oscillations was evaluated. Two participants were removed from the analyses because they lacked pre or post stimulation EEG recording. The analyses were calculated on the average of all the electrodes.

First, the percentage change in resting-state theta power pre- and poststimulation was calculated as the dependent variable. This analysis showed no significant effect of Stimulation, $F(1, 91) = 0.437$, $p = .510$, $\eta_p^2 = .005$; WMC Group, $F(1, 91) = 6.314 \times 10^{-4}$, $p = .980$, $\eta_p^2 = 6.939 \times 10^{-6}$; nor their interaction, $F(1, 91) = 0.312$, $p = .578$, $\eta_p^2 = .003$. Then, the analyses were performed during the task. The same percentage change in theta power pre- and poststimulation was calculated, but this time during the retention delay while participants performed the task. Then, it was introduced in a repeated-measures ANOVA with WMC Group and Stimulation as between-participants factors, and Task Load as a within-subject factor. This analysis revealed only a marginal trend in the Stimulation × Task Load interaction, $F(1, 91) = 3.678$, $p = .058$, $\eta_p^2 = .039$, falling to reach statistical significance. The overall difference between stimulation groups was nonsignificant, $F(1, 91) = 0.974$, $p = .326$, $\eta_p^2 = .011$. Descriptively, the sham group showed a greater increase in theta power than the theta stimulation group, especially in the low-load condition ($M_{\text{low-sham}} = 15.411\%$, $M_{\text{low-theta}} = -1.401\%$; $M_{\text{high-sham}} = 9.984\%$, $M_{\text{high-theta}} = 6.291\%$, see Figure 5). No main effects or interactions involving WMC Groups reached significance.

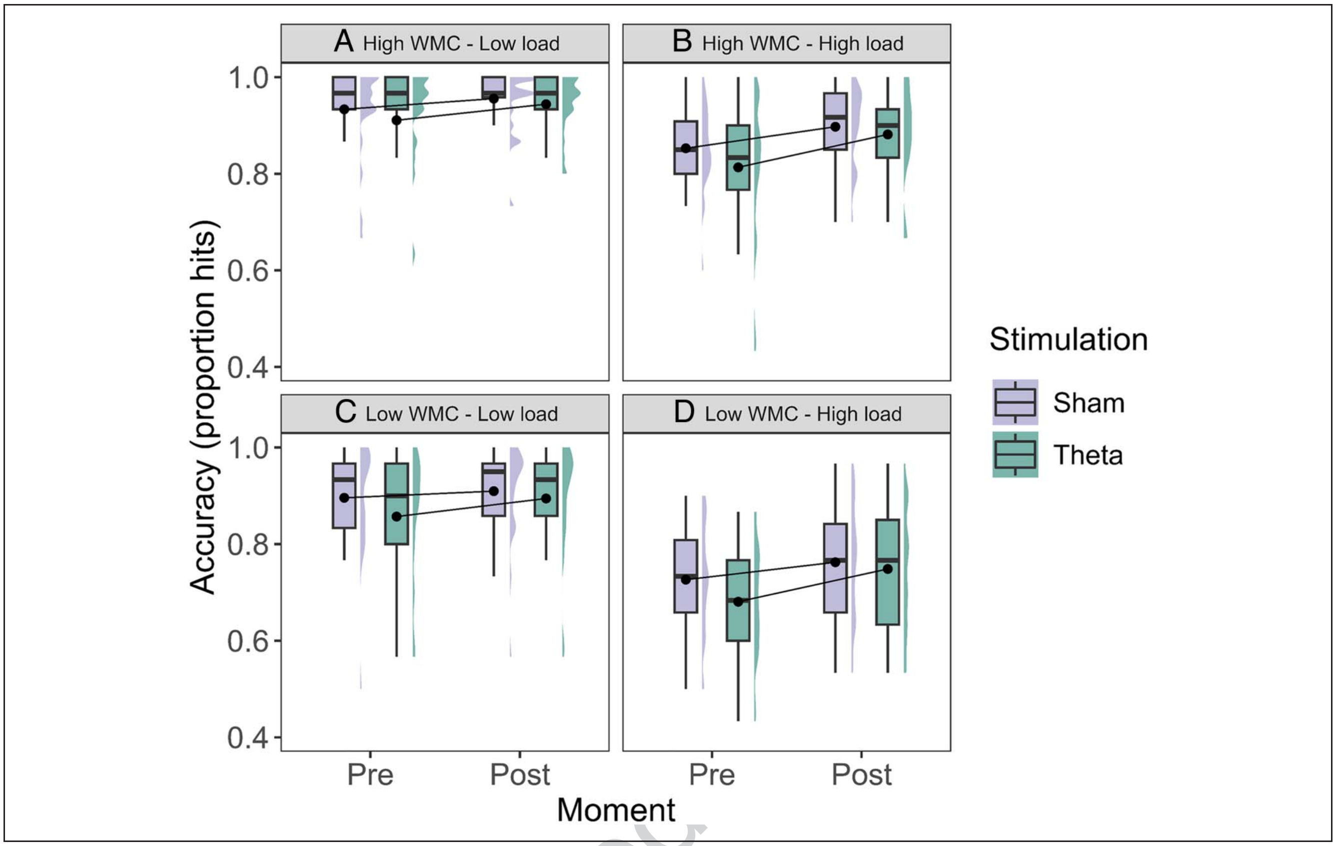

Figure 4. Nonsignificant effects of stimulation in accuracy, split by all the conditions: high WMC (upper row) or low WMC (lower row); low load (left column) or high load (right column); sham (purple) or theta (green) stimulation; and pre or post stimulation. A very similar pattern was observed in the rest of the measurements (i.e., RT, d', and K), but only ACC is plotted for simplicity, given the null effects of stimulation. In the box plots, the central line represents the median, and the black point indicates the mean. The lower and upper limits of the box plot represents the first and third quartiles, respectively. Error bars represent the standard error of the mean.

Mean Theta *gF* and Theta Peak Variations

First, the prediction that low WMC participants must exhibit a higher mean theta frequency (allowing less gamma to couple and, thus, less items maintained) was tested. To that end, the *gF* of the memory delay in the first EEG block (prestimulation) of both WMC groups were compared.[3] Again, the analyses were calculated on the average of all the electrodes. This analysis showed significant differences between the groups, $F(1, 93) = 10.621$, $p = .002$, $\eta_p^2 = .080$. However, the direction of the results was contrary to the theta–gamma coupling theory prediction: The high WMC participants exhibited a higher mean theta, compared with the low WMC participants ($M_{\text{lowWMC}} = 4.575$ Hz, $M_{\text{highWMC}} = 4.780$ Hz; see Figure 6). To test whether this result could depend on the high- or low-load trials, we again calculated *gF* but separately for three-load and five-load trials. Then, an ANOVA with Task Load and WMC Groups was performed again on the EEG block before stimulation, revealing a main effect of Task Load, $F(1, 93) = 21.672$, $p < .001$, $\eta_p^2 = .189$, but no interaction with WMC Group, $F(1, 93) = 0.110$, $p = .741$, $\eta_p^2 = .001$. The main effect of WM Load showed a result contrary to the theta–gamma coupling theory: High-load trials showed higher

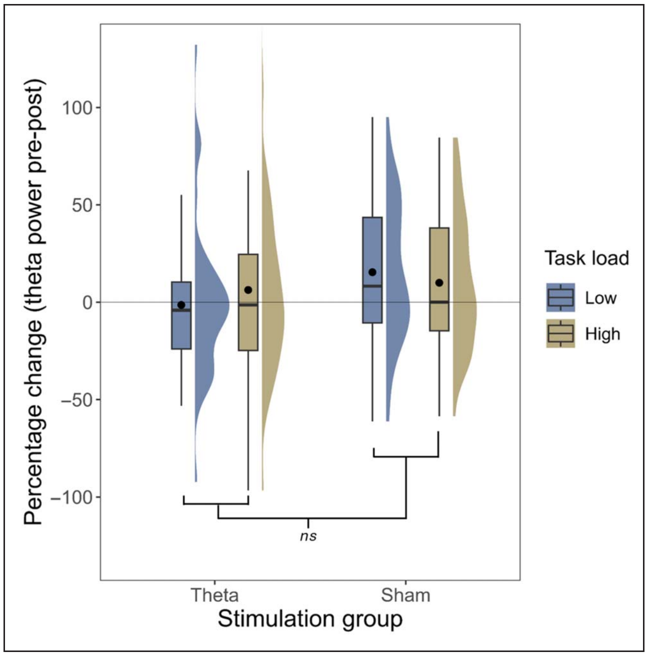

Figure 5. Nonsignificant Stimulation Group × Task Load interaction in percentage theta power change. Error bars represent the standard error of the mean.

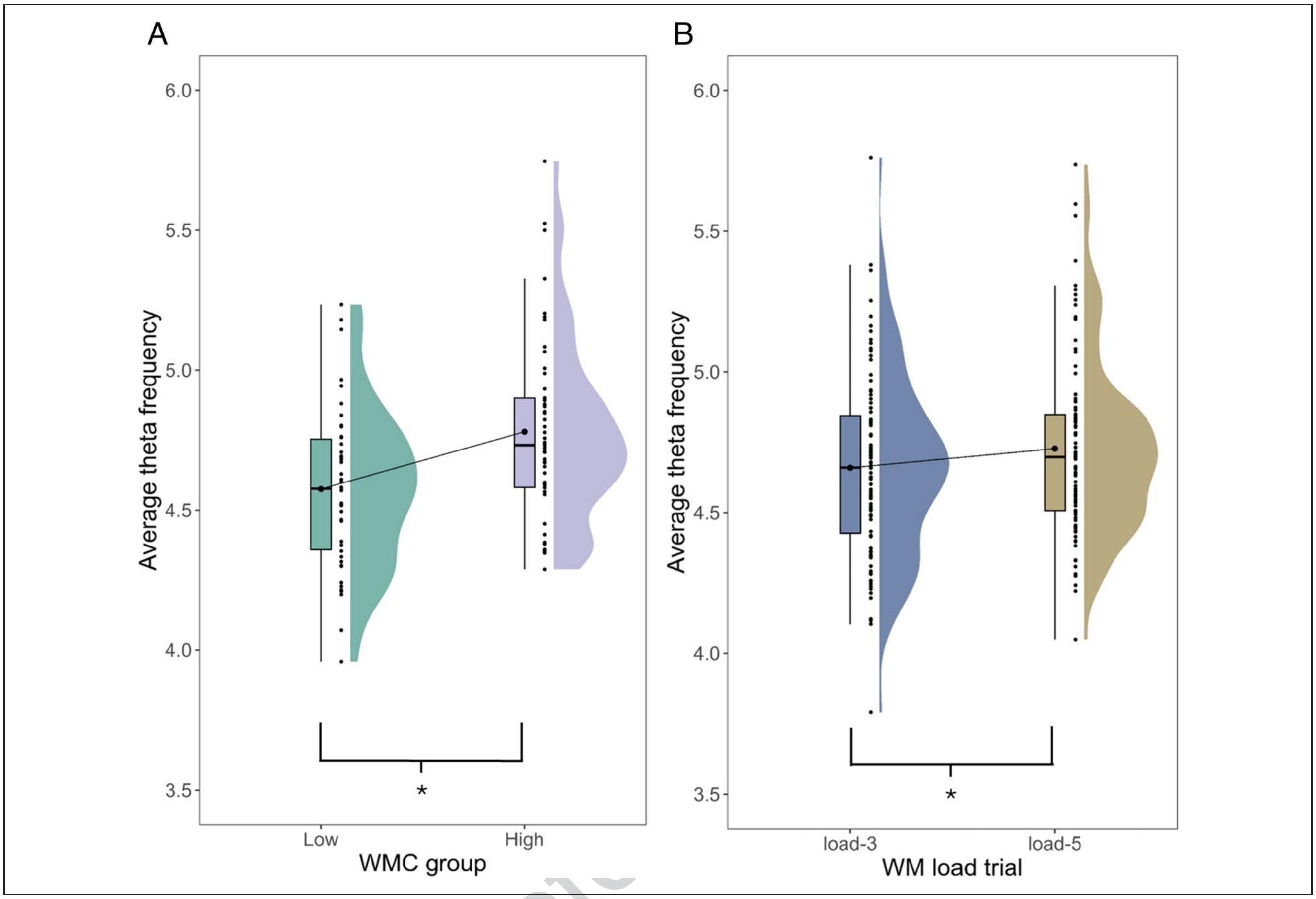

Figure 6. (A) Raincloud plots of mean theta *gF* during the retention delay pre stimulation in high and low WMC groups. (B) Raincloud plots of mean theta *gF* during the retention delay pre stimulation in high- and low-load trials. The small dark points represent the mean of each participant in each condition. The black point joined by a gray line represent the means of both conditions. The individual distributions for both conditions are represented in the split violin plots.

mean theta, compared with the low-load trials ($M_{\text{low-load}}$ = 4.659 Hz, $M_{\text{high-load}}$ = 4.727 Hz; see Figure 6).

When these analyses were performed on the theta peak, no effect reached statistical significance regarding pre stimulation differences between the WMC groups both during the task, $F(1, 95) = 0.211$, $p = .647$, $\eta_p^2 = .002$, or at resting, $F(1, 93) = 0.197$, $p = .658$, $\eta_p^2 = 2.383 \times 10^{-4}$.

Second, the efficacy of tACS to modulate theta frequency was tested. For this, the pre–post stimulation percentage change of the *gF* was calculated in both WMC groups during the task. Then, an ANOVA with WMC Group and Stimulation as between-participants factors and Percentage Change as dependent variable was calculated. Results show no significant effect of Stimulation, $F(1, 91) = 0.347$, $p = .557$, $\eta_p^2 = .004$, or WMC Group × Stimulation interaction, $F(1, 91) = 0.075$, $p = .785$, $\eta_p^2 = 8.254 \times 10^{-4}$. Raw EEG showed no significant change of the theta frequency in the last block of the task compared to the first block, $t(94) = 0.519$, $p = .473$, $d = 0.005$ (M_{first} = 4.681 Hz, M_{last} = 4.170 Hz), independently of the stimulation. Again, when this analysis was performed on theta peaks, no main effect of stimulation, $F(1, 91) = 1.557$, $p = .215$, $\eta_p^2 = .017$, or WMC × Stimulation interaction, $F(1, 91) = 0.884$, $p = .350$, $\eta_p^2 = .010$, reached statistical significance.

PLV between Stimulation Electrodes

Although it was not preregistered, changes in stimulation electrodes—F3 and P3—synchronization during the WM delay were evaluated by calculating the percentage change in PLV before and after stimulation, both in the sham and theta stimulation groups. Initially, this calculation was performed using all trials. This analysis showed an overall increase in PLV in both the theta and sham groups (M_{theta} = 9.14%, M_{sham} = 5.44%). However, the difference between the two groups was not significant, $F(1, 94) = 3.805$, $p = .054$, $\eta_p^2 = .039$. Because trials in which participants failed to respond correctly might exhibit lower synchronization, the same analysis was conducted using only the hit trials. Again, both groups showed an increase in PLV after the stimulation block (M_{theta} = 9.105%, M_{sham} = 5.495%), but differences between the two groups were not

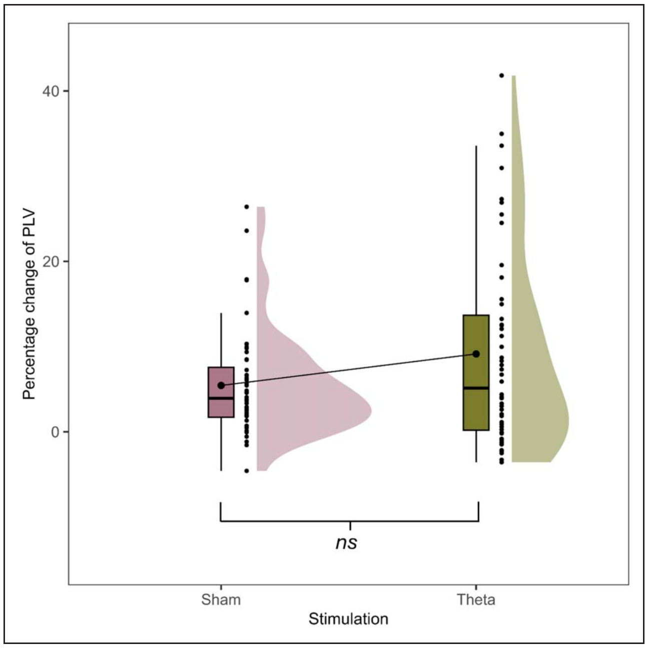

Figure 7. Raincloud plots of percentage change of PLV in sham and theta stimulation groups. No significant differences were observed across groups. The small dark points represent the mean of each participant in each condition. The light gray point joined by a gray line represent the means of both groups. The individual distributions for both stimulation groups are represented in the split violin plots.

statistically significant, $F(1, 94) = 3.812$, $p = .054$, $\eta_p^2 = .039$, with a greater increase in synchronization in the theta stimulation group (see Figure 7).

DISCUSSION

In the present study, we assess some of the predictions posited by the theta–gamma coupling model of WM. Specifically we assess whether slowing down theta frequency rhythms would facilitate WM performance. To this end, we applied a 4-Hz tACS with the aim of slowing down synchronized theta rhythms in the frontoparietal network. We also manipulated task difficulty (i.e., load), given previous studies that show tACS modulation effects primarily under challenging task conditions. The behavioral results revealed the successful manipulation of both WMC groups and task load. However, contrary to our hypotheses, participants receiving 4 Hz of theta tACS did not exhibit any benefits over the sham group. Importantly, this lack of a behavioral effect cannot be attributed to a ceiling effect, as the task was sensitive in the critical condition where effects were expected: The low WMC group in the high-load condition performed 0.75 accuracy. These null effects were observed across measures of RT, accuracy, d', and K.

As in Experiments 1 and 2A in Biel and colleagues (2022), we found no behavioral modulation after theta tACS in a delayed letter discrimination task similar as the one used by Polanía and colleagues (2012), that is, the easy trials of the task used in the present experiment. However, contrary to their Experiment 2B in which they observed an improvement in WM using a difficult 3-back task, we did not observe any modulation in more demanding trials. One aspect in which our experiment differs from that of Biel and colleagues (2022) and which could explain this divergence of results is that, besides item maintenance, the 3-back might require updating and controlling of WM representations (Gajewski, Hanisch, Falkenstein, Thönes, & Wascher, 2018; Rac-Lubashevsky & Kessler, 2016), as well as motor preparation (Pavlov & Kotchoubey, 2022). These central executive-dependent functions seems to be closely linked to frontoparietal theta synchronization (Sauseng et al., 2005, 2010; Hanslmayr et al., 2008). Therefore, one possibility is that tasks such as the 3-back—where executive control is involved—are more likely to be modulated by theta tACS. Against this argument, Vosskuhl and colleagues (2015) applied tACS and compared the effects of tACS on the 3-back task measured before and after stimulation and also found no modulation. However, the stimulation frequency was adapted to each participant and, on average, was close to 4 Hz (i.e., the same as we used), in contrast to the 6 Hz applied by Biel and colleagues (2022). Another possibility is that the theta modulation only shows benefits in *n*-back tasks with faster theta frequencies (Violante et al., 2017; but see Chander et al., 2016).

In this line, recent evidence from Kaiser and colleagues (2025) shows that a 5-Hz tACS selectively enhances hippocampal–cortical connectivity, suggesting that slower theta rhythms engage hippocampal network dynamics. This contrasts with findings indicating that slightly faster theta (∼6 Hz) may be more effective in facilitating frontoparietal connectivity (e.g., Biel et al., 2022; Violante et al., 2017; Polanía et al., 2012). Given this, it is possible that the 4-Hz stimulation applied in our study was not optimal for enhancing frontoparietal network activity, which may explain the absence of observable behavioral effects. This interpretation also contradicts what would be expected under the theta–gamma coupling model, which posits that slower theta rhythms should allow for a greater number of gamma cycles per theta cycle, thus enhancing WMC. However, our findings, together with previous null results using slow theta stimulation (e.g., Vosskuhl et al., 2015), suggest that the functional impact of theta frequency on WM might not be fully explained by this model alone and that different frequency ranges could engage distinct neural networks.

Contrary to our initial hypotheses, the EEG recordings did not reveal robust differences between stimulation groups. Using the present baseline correction free of other evident cognitive processes, we observed only a marginal effect of stimulation on theta power. Note that, when a baseline window closer to the maintenance interval was used (−600 to −100 msec), significant differences in power were observed between the active and sham groups. However, even in that analysis, the theta tACS group exhibited a close-to-zero increase in theta power compared with the sham group (see Supplements). This was an unexpected finding, as an increase in power at the stimulated frequency is typically seen after tACS in theta and other frequency bands (see Pavlov & Kotchoubey, 2022, and Vogeti, Boetzel, & Herrmann, 2022, for recent reviews). One explanation might be that theta stimulation may have attenuated the theta power increases typically observed after periods of attentional fatigue (Clayton, Yeung, & Cohen Kadosh, 2015). Another xpossible explanation is that it results from a mismatch between the individual's endogenous theta rhythm and the externally applied tACS frequency (Wischnewski & Schutter, 2017). This mismatch could lead to synaptic weakening (Vogeti et al., 2022; Vossen, Gross, & Thut, 2015; Zaehle, Rach, & Herrmann, 2010) or simply disrupt the individual's oscillatory activity (Voytek & Knight, 2015). In this line, Chander and colleagues (2016) observed a decrease in theta power (and WM performance), which was attributed to interference between the tACS stimulation and the endogenous oscillations. The present results show no power increment in the stimulated band, which might reflect a lack of synchronization between endogenous and exogenous oscillations and should be considered in future studies.

Second, contrary to the theta–gamma coupling theory and our preregistered hypothesis, we did not find that the high WMC group, which performed better on the task, exhibited a lower mean theta frequency before any stimulation. Instead, they showed a higher mean theta frequency compared with the low WMC group. This result was robust with respect to the baseline correction used. This pattern of results aligns more closely with an alternative model regarding the role of theta in the maintenance of information in WM (Van Vugt, Chakravarthi, & Lachaux, 2014; Herman, Lundqvist, & Lansner, 2013). According to this framework, a complete gamma burst represents a single item, and each theta cycle nests one gamma burst. When multiple items need to be maintained in WM, several theta cycles must be reactivated to refresh all the items, which might potentially explain the limited capacity of WM (Van Vugt et al., 2014). Faster theta cycles would therefore enable quicker refreshing of WM items, preventing their loss. A person capable of activating more items in a shorter time (i.e., with faster theta rhythms) should be able to maintain more information in their WM. Given the differences in mean theta frequency for the two WMC groups, the present results are more consistent with this explanation. Besides, according to the theta–gamma coupling model, theta frequency should be lower in high WMC individuals, which was not observed in the present data. In addition, theta frequency modulations observed in relation to the task difficulty manipulation were also contrary to the model, showing a higher mean frequency for the high-load trials. These findings raise questions about which specific hypotheses derived from the theta–gamma coupling theory can be reliably observed in human EEG studies (see also Maleninská et al., 2021).

Contrary to our hypothesis, our results show that the mean theta frequency was not reduced in the stimulation group compared with sham. According to the theta–gamma coupling model, this could explain the lack of behavioral effects, but the fact that no lower theta was observed in the high WMC group raises doubts about this reasoning. To be noted, in the context of the theta–gamma coupling model, tACS has been shown to reduce or increase theta power (Pahor & Jaušovec, 2018; Chander et al., 2016; Vosskuhl et al., 2015) or phase synchronization (Alekseichuk, Pabel, Antal, & Paulus, 2017; Chandler et al., 2017). However, only two studies have examined the frequency peak modulations after theta tACS. Kleinert and colleagues (2017) studied the theta modulations in resting state before and after the 6-Hz stimulation and only found alpha modulations but not for the theta band. Vosskuhl and colleagues (2015) found an amplitude increase at 6.7 Hz after theta stimulation even though the average frequency of applied stimulation was 4.23 Hz. Then, the present results advocated caution in the use of tACS as a way of modulating specific frequencies given that it might have no effect or an unexpected effect on frequencies different than the targeted ones.

Third, our exploratory analyses regarding the connectivity between the two stimulation electrodes initially showed a greater increase in phase synchrony following theta stimulation when a baseline close to the memory interval was used, consistent with previous findings (Alekseichuk et al., 2017; Chandler et al., 2017). However, this effect was only observed when error trials were excluded from the analyses. Besides, when a new baseline correction was used, no better phase synchronization was observed after theta stimulation (results only showed marginal effects). Although it might be expected that synchronization would be most evident in successful trials, the fact that this trend disappeared under another baseline correction reinforces the idea that the 4-Hz stimulation had no robust impact on frontoparietal dynamics. This scenario highlights the necessity for preregistered studies to confirm whether this tACS can reliably modulate long-range connectivity.

Lastly, the present work has several limitations. First, only a few frontoparietal electrodes were placed and analyzed but other studies have found relevant theta EEG information in other electrode locations (Aktürk et al., 2022; Chander et al., 2016; Vosskuhl et al., 2015). Related to that, the use of average reference with a low-density montage constitutes a methodological limitation (Yao, 2017; Nunez, 2010). However, the inspection of the data using reference to the hardware earlobe electrode revealed that it introduced substantial common noise that masked the oscillatory activity (see Supplemental Figure S2). As mentioned before, the comparison of the present results with those found by Biel and colleagues (2022) is limited given the difference in the task that were used and the frequency of stimulation. Other research could do a direct comparison between the results obtained using an *n*-back and a delayed letter response task, similar to Pahor and Jaušovec (2018). However, two previous studies that applied individualized theta stimulation (Aktürk et al., 2022; Vosskuhl et al., 2015) used mean stimulation frequencies that were very close to 4 Hz. Specifically, Vosskuhl and colleagues (2015) applied individualized downregulation of theta, with mean stimulation frequencies of 4.62, 4.12, and 3.73 Hz across different blocks. Similarly, Aktürk and colleagues (2022) applied stimulation at each participant's individual theta frequency minus 1 Hz, with a resulting mean stimulation frequency of approximately 4 Hz. Given these findings, our choice of the 4-Hz stimulation may not be far from the relevant frequency range for modulating theta activity. On the other hand, the EEG analyses in the present work were restricted to the maintenance interval (0–2500 msec). Studying the encoding phases was not feasible in the current design given the uneven durations of the three-load and five-load trials. Future research could employ designs with fixed encoding durations (e.g., presenting five stimuli in all trials but cueing only a subset for retention) to properly study the encoding phase using epochs of equal length. This fix would also allow for an equal baseline correction between conditions in future studies. Finally, it is important to note that our analysis of EEG aftereffects of tACS was restricted to the theta range (i.e., power, frequency and phase locking). Given evidence that tACS can modulate oscillatory activity at frequencies other than the stimulation frequency (Wischnewski, Alekseichuk, & Opitz, 2023; Wischnewski & Schutter, 2017; Helfrich et al., 2014), future work should investigate effects across a broader frequency range.

In conclusion, the present study shows that a focal in-phase 4-Hz tACS does not modulate performance during a WM task that primarily relies on the maintenance of information, even when task difficulty and baseline WMC are controlled. Electrophysiological results indicated no power increase following stimulation. This lack of effect might be due to insufficient or mismatched synchronization between the endogenous and exogenous frequency rhythms, or between the frequency and the targeted network. EEG data also revealed (1) a higher mean theta frequency in high WMC participants compared with low WMC ones and (2) a higher mean theta frequency in high-load trials, where more items had to be maintained, compared with low-load trials. These results are not consistent with the theta–gamma coupling model. Therefore, the theta–gamma coupling model, which is the most established framework for explaining WM maintenance, may need to be revisited.

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Data Availability Statement

The methods and hypotheses were preregistered in Open Science Framework before data collection on March 21, 2023 (https://osf.io/ghqk6/). At the beginning of data collection, on May 10, 2023, the stimulation protocol was updated in the preregistration due to technical issues with an initial device that had to be replaced. All materials, data, and code are available at https://osf.io/9swk7/, where deviations from the original protocol are also disclosed and explained. Supplemental Material can be accessed on this article's homepage: https://doi.org/10.1162/JOCN.a.2594.

Author Contributions

Miriam Tortajada: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Software; Visualization; Writing—Original draft; Writing—Review & editing. Julio Rodríguez-Larios: Formal analysis; Methodology; Software; Visualization; Writing—Review & editing. Victor Martínez-Pérez: Conceptualization; Investigation; Writing—Review & editing. Lucia B. Palmero: Conceptualization; Investigation; Writing—Review & editing. Luis J. Fuentes: Conceptualization; Funding acquisition; Project administration; Supervision; Writing—Review & editing. Guillermo Campoy: Conceptualization; Formal analysis; Methodology; Supervision; Visualization; Writing—Review & editing.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this paper report its proportions of citations by gender category to be: M/M = .6; W/M = .271; M/W = .057; W/W = .071.

Notes

1. Following a reviewer's suggestion to avoid cognitive overlap during the stimulus presentation phase, the baseline window

was shifted from the preregistered −600- to −100-msec interval to the initial fixation cross. To ensure transparency, analyses with the initial baseline are also available in the Supplements.
2. This must be interpreted considering the results in ACC, where the low WMC group performed worse than the high WMC group, especially in the most difficult trials. This might indicate that high WMC participants were slower because they were able to maintain all the information in WM, and, to respond, they needed to perform a slower and more systematic search within their WM. In contrast, the fast response and low ACC of the low WMC group suggest that their responses were based on a faster and less accurate procedure, probably relying on familiarity due to the difficulty in maintaining all the information in their WM.
3. All the EEG analyses were performed on all the trials, but the same results were observed when the analyses were performed only on the hit trials (i.e., trials with successful item maintenance).

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