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Dual-montage high-definition transcranial direct current stimulation (HD-tDCS) modulates the neural dynamics serving working memory

Peihan J. Huang^{a,b}, Yasra Arif^a, Jake J. Son^{a,c}, Jason A. John^a, Maggie P. Rempe^{a,c}, Kellen M. McDonald^{a,b}, Lauren K. Webert^a, Grant M. Garrison^a, Hannah J. Okelberry^a, Kennedy A. Kress^a, Nathan M. Petro^a, Tony W. Wilson^{a,b,c,*}

^aInstitute for Human Neuroscience, Boys Town National Research Hospital, Boys Town, NE, USA

^bDepartment of Pharmacology & Neuroscience, Creighton University, Omaha, NE, USA

^cCollege of Medicine, University of Nebraska Medical Center (UNMC), Omaha, NE, USA

Abstract

Verbal working memory (WM) is a critical cognitive construct supporting a broad range of daily functions. Neuroimaging studies have highlighted the involvement of prefrontal-occipital circuitry in WM, but specific regional contributions and possible laterality effects remain unclear. Transcranial direct current stimulation (tDCS) is an emerging technique that noninvasively modulates the excitability of neural populations, with studies showing stimulation effects on both local and distant but connected cortices. Herein, we utilized a novel dual-montage, high-definition tDCS (HD-tDCS) approach to evaluate the impact on functional brain dynamics and WM performance. Forty-five healthy adults underwent dual-montage HD-tDCS with 2.0 mA anodal stimulation applied over the midline occipital cortices and either the left or right dorsolateral prefrontal cortices (DLPFC) concurrently, or sham to both sites during three sessions. Following stimulation, participants completed a verbal WM task during magnetoencephalography (MEG). Whole-brain, voxel-wise maps were subjected to 1×3 repeated measure ANOVAs to probe stimulation effects. We found that left DLPFC-occipital stimulation induced stronger theta responses in the left superior temporal cortices, left supramarginal gyrus, left angular gyrus, and the right parietal cortices, while attenuated alpha responses were observed in the bilateral parietal

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*Corresponding author at: Institute for Human Neuroscience, Boys Town National Research Hospital, USA. tony.wilson@boystown.org (T.W. Wilson).

CRedit authorship contribution statement

Peihan J. Huang: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Conceptualization. **Yasra Arif:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Jake J. Son:** Writing – review & editing, Resources, Funding acquisition. **Jason A. John:** Writing – review & editing, Project administration, Data curation. **Maggie P. Rempe:** Writing – review & editing, Resources, Methodology. **Kellen M. McDonald:** Writing – review & editing, Project administration, Data curation. **Lauren K. Webert:** Writing – review & editing, Project administration, Data curation. **Grant M. Garrison:** Writing – review & editing, Project administration, Data curation. **Hannah J. Okelberry:** Writing – review & editing, Project administration, Data curation. **Kennedy A. Kress:** Writing – review & editing, Project administration, Data curation. **Nathan M. Petro:** Writing – review & editing, Supervision, Project administration, Methodology. **Tony W. Wilson:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

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cortices following right compared to left DLPFC-occipital stimulation and sham. Additionally, both active stimulation montages modulated oscillatory responses in the bilateral inferior frontal, the right lateral occipital cortices and other critical WM network regions during the encoding and maintenance phases. In conclusion, our results show that dual-montage anodal HD-tDCS differentially modulates spectrally and temporally distinct oscillatory responses, suggesting clear functional dissociations between left and right prefrontal regions during WM processing. These findings highlight the potential of tDCS in advancing our understanding of the unique contribution of each region in the network, which long-term could inform clinical interventions.

Keywords

Magnetoencephalography (MEG); Dual-montage; Transcranial direct current stimulation (tDCS); Working memory (WM); Dorsal lateral prefrontal cortex (DLPFC)

1. Introduction

Working memory (WM) is a core cognitive function, essential for daily activities that require the temporary storage and manipulation of information (Baddeley, 2010). Numerous tasks we perform, such as remembering a verification code or completing mental calculations, rely on WM to hold representations “in mind” and retrieve and organize memories over a short time period. Both spiking and persistent neural activity in the prefrontal cortices have been recognized as critical neural substrates, likely serving the top-down attentional control of parietal-occipital cortices required to complete such tasks (Curtis and D’Esposito, 2003; D’Esposito and Postle, 2015; Funahashi, 2017; Fuster, 2009). Additionally, robust hemispheric lateralization has been found in children and adults studies, with greater left hemispheric activation during verbal WM tasks and greater right hemispheric activation in homologous regions in spatial WM paradigms (Nagel et al., 2013; Thomason et al., 2009). However, despite the well-established contribution of the dorsolateral prefrontal cortices (DLPFC) to verbal WM, there is not a full consensus on the functional significance of DLPFC laterality, particularly whether it is domain-general or -specific, and whether such laterality results in differential modulation of posterior cortices supporting verbal WM processes.

Neurophysiological studies have contributed significantly to our understanding of how neural oscillations within the theta, alpha and gamma frequency ranges support verbal WM operations in the visual modality. The first stage, WM encoding, begins with sensory transformations in the visual cortices, which are then carried through the visual hierarchy by cortical traveling wave-like activity (Heinrichs-Graham and Wilson, 2015; Muller et al., 2018). This progression through the visual hierarchy occurs with widespread feedback and feedforward processes regulated by cortical oscillatory dynamics (King and Wyart, 2021; Mohan et al., 2024; Muller et al., 2018). Sustained oscillatory alpha and beta responses have been widely reported and appear to be critical to both WM encoding and maintenance phases (Heinrichs-Graham and Wilson, 2015; Pavlov and Kotchoubey, 2022; Proskovec et al., 2016; A.L. 2018; A.L. 2019; Wiesman et al., 2021; Wilson et al., 2017). These responses first emerge in the bilateral occipital cortices and progress anteriorly to the temporal and

parietal regions, including widespread involvement of language-related cortices (Heinrichs-Graham and Wilson, 2015, 2015; A.L. Proskovec et al., 2019; Wiesman et al., 2021). A recent study has proposed that short-term Hebbian synaptic plasticity (Faghihi and Moustafa, 2015; Takeuchi et al., 2014; Wang et al., 2013; Ziegler et al., 2015) may play a critical role in maintaining WM representations (Lansner et al., 2023), by strengthening connections between neural circuits that encode specific task-related information, but the key mechanisms and processes remain poorly understood, especially in humans.

To better understand these processes and work toward improving them, a number of studies have leveraged noninvasive brain stimulation techniques, such as transcranial direct current stimulation (tDCS), to assess and potentially alter various cognitive processes, including WM (Assecondi et al., 2021; Hill et al., 2016; Moghadas Tabrizi et al., 2023; Toth et al., 2024). tDCS is thought to modulate subthreshold membrane potential through axonal terminal polarization, with studies suggesting that anodal stimulation may induce long-term potentiation and increase cortical excitability (Fertonani and Miniussi, 2017; Stagg et al., 2009). It has been further proposed that the modulatory effects of tDCS on synaptic strength may occur through endogenous voltage-dependent Hebbian plasticity, specific to the active pathway (Kronberg et al., 2020). In studies to date, the DLPFC, parietal, and the occipital cortices have been primary stimulation targets, as all are involved in WM and attention processing. Previous brain stimulation research targeting the occipital cortices during a visual attention reorientation task found that anodal stimulation-induced stronger gamma responses in the occipital cortices relative to both cathodal and sham conditions (Arif et al., 2022). There have also been recent WM stimulation studies targeting the parietal cortices, which found robust modulatory effects of tDCS on theta and alpha oscillations within key WM regions during both encoding and maintenance (Arif et al., 2024). Additionally, studies have applied left versus right DLPFC anodal stimulation to assess the effects on visual selective attention and WM processes and found significant effects of left DLPFC stimulation on task-related theta and alpha oscillations, which further scaled with reaction time (Koshy et al., 2020; Spooner, Eastman, et al., 2020). Many of these studies and others have examined stimulation induced effects using a whole-brain approach and, taken together, suggest that the modulatory effects of tDCS on neural activity affect both local and distant neural populations (Erker et al., 2024; P. J. Huang et al., 2025; McDermott et al., 2019; Son et al., 2025; Wiesman et al., 2018; Wilson et al., 2018), and likely rely on the interaction with endogenous electric fields. Thus, dual-montage or network-level tDCS could theoretically improve stimulation efficacy compared to single site stimulation alone, as simultaneously driving two functionally connected regions may strengthen their functional interactions over time and lead to greater modifications in neuronal excitability based on basic Hebbian principles. In addition, dual-montage approaches may provide greater insight on the mechanisms underlying distant effects of tDCS, as well as the impact of local stimulation polarity. While no studies to date have applied simultaneous DLPFC-occipital stimulation to evaluate modulatory effects on the brain regions and dynamics underlying WM processes, several studies have used dual-montage approaches. For example, a TMS-EEG study applied tDCS to the frontal and parietal cortices during a WM task and found that a dual-site montage was more effective in modulating WM-related neural responses (Hill et al., 2018). Additionally, several studies have applied simultaneous

anodal stimulation of ipsilateral M1 and DLPFC and reported improved motor function, which may reflect increased interactions between functionally connected regions serving task performance (Achache et al., 2018; Vaseghi et al., 2015). Thus, there is preliminary evidence suggesting that dual-montage approaches may be a particularly promising direction for tDCS research.

Beyond the issue of single versus dual-montages, a significant challenge in tDCS research has been the variability in reported outcomes, both in terms of neural activity and behavioral performance. A recent meta-analysis assessed the effects of left prefrontal tDCS on WM performance and the factors that contribute to such heterogeneous findings in the tDCS literature, with the key conclusions being that within-subject designs were more consistent and that there was a trend towards improvements in WM following anodal high-definition tDCS (HD-tDCS) of the left PFC compared to sham (Müller et al., 2022). Previous studies examining the role of the DLPFC in WM have often utilized conventional bipolar tDCS montages (Framorando et al., 2021; Giglia et al., 2014; Meiron and Lavidor, 2013), which are a robust approach for delivering current but often result in diffuse effects on the cortex. In contrast, HD-tDCS utilizes smaller electrodes in a ring configuration and allows for greater focality, thereby enabling more precise targeting of cortical regions and minimal extraneous stimulation. To this end, we applied anodal stimulation simultaneously to the DLPFC and occipital cortices to assess the effect of network level tDCS on the neural dynamics serving WM function in healthy adults. We hypothesized that parallel stimulation of the left prefrontal and midline occipital cortices would differentially alter neurophysiological responses within left hemispheric language regions serving verbal WM processing compared to sham and simultaneous right prefrontal and midline occipital stimulation. In addition, we hypothesized that other critical WM regions would be altered by both left- and right prefrontal-occipital stimulation relative to sham.

2. Methods

2.1. Participants

Fifty healthy adults (27 females) between the ages of 20 and 36 years ($M = 26.35$, $SD = 3.91$) were enrolled in this study. Exclusionary criteria included any neurological or psychiatric disorders, any medical illness known to affect central nervous system function (e.g., Lupus, HIV infection), history of head trauma, current substance abuse, and any nonremovable ferromagnetic implants that would interfere with MEG data acquisition. The study protocol (BTNRH-20–26-XP) was approved by the Boys Town National Research Hospital's Institutional Review Board (IRB). A full description of the study was provided to all participants, and written informed consent was obtained from each participant at the beginning of the first visit.

2.2. High-definition transcranial direct current stimulation (HD-tDCS)

The high-density MxN-65 transcranial electrical stimulation system (Soterix Medical, New York, NY, USA) was used to deliver dual-montage HD-tDCS. Each 4×1 montage was comprised of an anode-center electrode surrounded by four cathode electrodes. Participants completed three visits following a randomized crossover design, with an interval of

approximately a week between each visit ($M = 10.61$ days, $SD = 6.12$ days; Fig. 1). During the two active stimulation visits, 20 min of 2.0 mA anodal HD-tDCS was administered to the midline occipital cortices (Oz) simultaneously with 20 min of 2.0 mA anodal HD-tDCS of either the left (F3) or right (F4) DLPFC. Each 20-minute stimulation window began with a 30-s ramp-up period. This custom dual-montage approach was designed to deliver relatively focal stimulation to both the primary visual cortices in the calcarine fissure and the DLPFC, which are two of the most distant nodes in the brain network serving verbal WM. During sham visits, no stimulation was delivered outside of the ramping period and the placement of DLPFC montage (left versus right) was counter-balanced and pseudorandomized across individuals. During tDCS stimulation, participants performed a multisource interference task, which kept them mentally engaged and minimized the variability of brain state during each visit. Participants and all researchers involved in data processing were kept blinded to the stimulation condition. Each electrode had a diameter of 12 mm, was comprised of Ag/AgCl, and was positioned using the International 10/20 system (Klem et al., 1999). The transformation of the electrode position to cortical projection points in MNI space was based on a probabilistic distribution method (Okamoto et al., 2004; Okamoto and Dan, 2005) that has been used in many transcranial stimulation studies (Arif et al., 2020, 2022, 2023; Koshy et al., 2020; Spooner et al., 2020). To quantify the intensity and focality of the stimulation, current flow modeling was performed using the ROAST software implemented in MATLAB, with tissue conductivities based on the literature (in S/m units, grey matter = 0.276, white matter = 0.126, CSF = 1.65, skull = 0.01, skin = 0.465, air = 1×10^{-7} , gel = 0.3, electrodes = 5.8×10^7 ; Datta et al., 2009; Huang et al., 2013, Y. 2018, Y. 2019).

2.3. Experimental paradigm

After each stimulation session, participants completed a verbal WM paradigm during MEG. Briefly, a fixation cross was presented centrally within a 2×3 grid for a jittered period of 1.5 ± 0.2 s. An array of six consonants then appeared for 2.0 s (i.e., encoding phase) and participants were instructed to remember these letters. The consonants then disappeared, with the empty grid remaining on the screen for 3.0 s during the maintenance phase. A single probe was then presented for 0.9 s and participants were instructed to respond as to whether the probe letter was among the six consonants presented during the encoding phase. For clarity, the location of the probe letter during retrieval remained constant across trials, but the probe itself could be any of the six letters (or none of the letters in out-of-set trials) that appeared in the encoding grid during the specific trial. Participants pushed a button with their right index finger during in-set trials, and their right middle finger during out-of-set trials. In total, participants completed a total of 128 trials that were pseudorandomized among an equal number of in-set and out-of-set trials, with an overall recording time of approximately 16 min (Fig. 1).

2.4. MEG data acquisition

MEG data were acquired and preprocessed following an established data analysis pipeline that is described in detail elsewhere (Wiesman and Wilson, 2020). All recordings were conducted in a two-layer magnetically-shielded VACOSHIELD room (Vacuumschmelze, Hanau, Germany). Neuromagnetic responses were sampled continuously at 1 kHz, with an acquisition bandwidth of 0.1–330 Hz, using a MEGIN TRIUX Neo MEG system (Helsinki,

Finland) with 306 sensors, equipped with 204 planar gradiometers and 102 magnetometers. Each participant's MEG data were individually corrected for head motion and subjected to noise reduction using the signal space separation method with temporal extension (Taulu and Simola, 2006).

2.5. Structural MRI processing and MEG co-registration

Preceding MEG measurement, five continuous head position indicator (cHPI) coils were attached to the participant's head and digitized, together with the scalp surface and the three fiducial points using a 3-D digitizer (FASTRAK; Polhemus Navigator Sciences, Colchester, VT). Once the participant was positioned for MEG recording, an electric current with a unique frequency label (e.g., 322 Hz) was fed to each of the coils. This induced a measurable magnetic field and allowed each coil to be localized in reference to the sensors throughout the recording session. Since the coil locations were also known relative to the fiducial markers, all MEG measurements could be transformed into a common coordinate system. With this coordinate system, each participant's MEG data were co-registered with structural T1-weighted MRI data prior to source-space analysis using BESA MRI (Version 2.0). These T1-weighted MRI images were acquired using a Siemens Prisma 3T MRI scanner with a 32-channel head coil and a 3D MP-RAGE sequence with the following parameters: TR = 2400 ms; TE = 2.05 ms; flip angle = 8°; FOV = 256 mm; slice thickness = 1 mm; voxel size = 1 mm³; 192 slices. The structural MRI volumes were aligned parallel to the anterior and posterior commissures and transformed into standardized space. Following source analysis (beamforming), each participant's MEG functional images were also transformed into standardized space using the same transformation matrix that was previously applied to the structural MRI volume and spatially resampled.

2.6. MEG preprocessing and time-frequency analyses

Cardiac and ocular artifacts were removed from the data using signal space projection (SSP), which was accounted for during source reconstruction (Uusitalo and Ilmoniemi, 1997). The continuous magnetic time series was filtered between 0.5 and 200 Hz and divided into epochs of 7.2 s duration, with the baseline being defined as -0.4 to 0.0 s before the encoding grid onset. The epochs that contained artifacts were rejected using a fixed threshold method that was based on the highest amplitude and/or gradient values relative to the full distribution across all trials for each participant. This approach was employed to minimize the impact of individual differences in sensor proximity and head size, which strongly affect MEG signal amplitude. Across all conditions and participants, the average amplitude threshold was 1070.24 fT/cm (SD = 295.80) and the average gradient threshold was 204.40 fT/(cm*ms) (SD = 97.88). On average, a total of 86.02 (SD = 11.22) artifact free trials per stimulation condition and participant were used for further analysis. A 1 × 3 repeated measures analysis of variance (RM-ANOVA) revealed no significant differences in the number of trials accepted by stimulation condition ($F[2,82] = 0.732, p = .484$), ensuring that our statistical comparisons were not biased by differences in trial count.

Artifact free epochs were transformed into the time-frequency domain using complex demodulation. The resulting power estimations per sensor were averaged over trials to generate time-frequency plots of mean spectral density. These sensor-level data were

normalized per time-frequency bin using the respective bin's baseline power, calculated using the mean power during the baseline period (−0.4 to 0.0 s). The specific time-frequency windows used for imaging were determined via statistical analysis of the sensor-level spectrograms across the entire array of gradiometers. Each data point in the spectrogram was initially evaluated using a mass univariate approach based on the general linear model. To reduce the risk of false positives results while maintaining reasonable sensitivity, a two-stage procedure was followed to control for Type I error. In the first stage, two-tailed paired-sample *t*-tests against baseline were performed on each data point during the encoding and maintenance windows and the output time series of *t*-values was thresholded at $p < .05$ to define time-points containing potentially significant oscillatory deviations across all participants. In stage two, time-frequency bins that survived the threshold were clustered with temporally or spectrally neighboring time-frequency bins that were also above the threshold. The cluster values were then derived by summing the *t*-values of all data points in the cluster. Nonparametric permutation testing was then used to derive a distribution of cluster values, and the significance level of the observed clusters (from Stage 1) were tested directly using this distribution (Ernst, 2004; Maris and Oostenveld, 2007). For each comparison, at least 10,000 permutations were computed to build a distribution of cluster values. Note that the goal of our sensor-level analyses were to identify the time-frequency windows where there were significant task-related changes in MEG signal strength during the encoding and maintenance phases relative to the baseline period for subsequent beamforming analyses. We did not compare the different stimulation montages at the MEG sensor-level because we were most interested in stimulation-induced changes at the cortical level and conducting the same statistical comparisons at both the sensor- and source-level can lead to inflated Type I error and is generally discouraged (Gross et al., 2013; Kriegeskorte et al., 2009).

2.7. MEG source imaging and statistics

Neural responses were imaged using the dynamic imaging of coherent sources approach, which is an extension of the linearly constrained minimum variance vector beamformer (Gross et al., 2001). Spatial filters were applied in the time-frequency domain to calculate voxel-wise source power for the entire brain volume. The single images were derived from the cross-spectral densities of all combinations of MEG gradiometers calculated over the time-frequency window of interest, and the solution of the forward problem for each location on a grid specified by the input voxel space. Following convention, we computed noise normalized source power in each voxel using active (i. e., task) and passive (i.e., baseline) periods of equal duration and bandwidth at an isotropic resolution of 4.0 mm. Such images are referred to as pseudo-*t* maps, with units (i.e., pseudo-*t*) that reflect noise-normalized power differences per voxel. All source imaging used the Brain Electrical Source Analysis (BESA version 7.1) software. The resulting 3-D whole-brain maps were subjected to 1×3 repeated-measures ANOVAs, with the HD-tDCS configurations (i.e., montages) as the three-level within-subjects factor to assess the significant neural oscillatory response differences among the HD-tDCS conditions. To ensure our pseudo-randomization of visit/stimulation montage order was successful in avoiding order effects, we conducted additional testing by regressing out the effect of visit order and computing the same statistical models using the residuals. The results of these tests were virtually identical, so we focus on the

original model (without visit order) for simplicity in the results section. To account for multiple comparisons, we utilized a cluster-extent based thresholding method by setting an initial threshold of $p < .005$ to identify significant clusters in the whole-brain maps, accompanied by a stringent cluster (k) threshold of at least 12 contiguous voxels (> 768 mm) based on the theory of Gaussian random fields (Poline et al., 1995; Worsley et al., 1999; Worsley et al., 1996). Whole-brain statistics were performed using the Rstatix package in R studio (Version 1.4.1717). All follow-up post hoc tests were performed using the SPSS software (V29). Values that were three standard deviations above or below their respective group means were considered outliers and removed from the analysis.

3. Results

3.1. Behavioral analysis

Five participants were not able to complete all three visits. Of the remaining 45 participants, three were excluded from our analysis due to low accuracy (i.e., 3 SDs below the mean). Thus, 42 participants (24 females) were included in the final analysis (range: 20–36 years ($M = 26.54$; $SD = 3.85$; all right-handed).

Participants performed well on the verbal WM task (Accuracy (%): left DLPFC-occipital: $M = 78.9$, $SD = 1.5$, 95 % CI [75.9, 81.8]; right DLPFC-occipital: $M = 80.2$, $SD = 1.45$, 95 % CI [77.4, 83.1], sham: $M = 78.6$, $SD = 1.5$, 95 % CI [75.4, 81.7]; Reaction time (ms): left DLPFC-occipital: $M = 741.78$, $SD = 18.679$, 95 % CI [704.06, 779.50]; right DLPFC-occipital: $M = 735.69$, $SD = 19.00$, 95 % CI [697.32, 774.06], sham: $M = 729$ ms, $SD = 18.37$, 95 % CI [691.91, 766.11]). Two 1×3 RM-ANOVAs were conducted (accuracy and reaction time) with behavioral performance during the task as the dependent variable and stimulation configuration as the independent within-subject variables. No significant effect of stimulation was found on accuracy ($F[2,82] = 1.013$, $p = .368$, $\eta^2 = 0.024$) or reaction time ($F[2,82] = 0.979$, $p = .380$, $\eta^2 = 0.023$).

3.2. MEG sensor-level analyses

We observed robust oscillatory responses across all participants and stimulation conditions. Robust increases in power relative to baseline were found in the theta (4 – 8 Hz; 0 – 0.25 s) and gamma bands (72 – 80 Hz; 0.1 – 0.3 s) following encoding grid onset ($p < .001$, corrected). In addition, there were sustained alpha oscillations (8–13 Hz; decreases relative to baseline) throughout the early encoding (0.3 – 1.1 s), late encoding (1.1 – 1.9 s), and early maintenance (2.0 – 2.4 s) periods ($p < .001$, corrected). Significant increases in alpha (11 – 15 Hz; 2.6 – 3.4 s) and gamma power (52 – 74 Hz; 2.3 – 2.5 s) were also detected during the maintenance period ($p < .001$, corrected; Fig. 2). These significant time-frequency windows were imaged using a beamformer. Longer duration windows were divided into 0.4 s non-overlapping time windows for imaging, which corresponded to the baseline period (–0.4 – 0.0 s).

3.3. Whole-brain oscillatory maps: theta encoding responses

To assess potential stimulation effects on the whole-brain oscillatory maps, 1×3 RM-ANOVAs were conducted. For the theta encoding responses (4 – 8 Hz; 0 – 0.25 s),

significant stimulation effects were found in the left angular gyrus ($F[2,74] = 9.158$, $p < .001$, corrected, $\eta^2 = 0.198$), right parietal cortex ($F[2,74] = 9.259$, $p < .001$, corrected, $\eta^2 = 0.200$), left superior temporal ($F[2,72] = 8.436$, $p < .001$, corrected, $\eta^2 = 0.190$), and the left supramarginal gyrus ($F[2,72] = 8.249$, $p < .001$, corrected, $\eta^2 = 0.186$). Post hoc testing revealed that theta oscillations were stronger during both active stimulation conditions compared to sham in the left supramarginal gyrus (left DLPFC: 95 % CI [.222, .918], $p = .001$; right DLPFC: 95 % CI [.150, .834], $p = .005$), left angular gyrus (left DLPFC: 95 % CI [.297, .998], $p < .001$; right DLPFC: 95 % CI [.071, .732], $p = .017$), and the right parietal cortices (left DLPFC: 95 % CI [.294, .995], $p < .001$; right DLPFC: 95 % CI [.249, .940], $p < .001$; Fig. 3). Furthermore, left DLPFC-occipital stimulation induced stronger theta responses in the left superior temporal gyrus relative to both right DLPFC-occipital stimulation (95 % CI [.255, .958], $p < .001$) and sham (95 % CI [.217, .913], $p = .001$; Fig. 3).

3.4. Whole-brain oscillatory maps: alpha and gamma encoding responses

To examine alpha oscillations during encoding, we first imaged the significant time-frequency window in 0.4 s intervals and then averaged the whole-brain images across the early (0.3 – 1.1 s) and late (1.1 – 1.9 s) alpha encoding windows per person. During the late encoding window, significant effects of stimulation were found in the left superior parietal ($F[2,72] = 7.024$, $p = .002$, corrected, $\eta^2 = 0.163$), right superior parietal ($F[2,72] = 8.577$, $p < .001$, corrected, $\eta^2 = 0.192$), right cerebellum ($F[2,74] = 7.073$, $p = .002$, corrected, $\eta^2 = 0.160$), and right inferior frontal cortices ($F[2,74] = 7.719$, $p < .001$, corrected, $\eta^2 = 0.173$). Post hoc testing revealed weaker alpha oscillations (i.e., less negative relative to baseline) following right DLPFC-occipital stimulation compared to sham in the left superior parietal cortex (95 % CI [.287, .996], $p < .001$; Fig. 4). Alpha oscillations were also weaker in the homologous right superior parietal cortices following right DLPFC-occipital stimulation compared to both sham (95 % CI [.377, 1.107], $p < .001$) and left DLPFC-occipital stimulation (95 % CI [.228, .926], $p = .001$). Finally, alpha oscillations were weaker in the right inferior frontal gyrus (left DLPFC: 95 % CI [.205, .888], $p = .002$; right DLPFC: 95 % CI [.244, .935], $p < .001$) and right cerebellum following both active stimulations compared to sham (left DLPFC: 95 % CI [.135, .806], $p = .006$; right DLPFC: 95 % CI [.265, .959], $p < .001$; Fig. 4). No significant effects of stimulation were found during the early alpha encoding window nor the gamma encoding window (i.e., 72–80 Hz; 0.1 to 0.3 s).

3.5. Whole-brain oscillatory maps: alpha and gamma maintenance responses

During the maintenance phase, we found significant effects of stimulation on the early alpha responses (8–13 Hz, 2.0 to 2.4 s) in the left inferior frontal cortices ($F[2,74] = 7.229$, $p = .001$, corrected, $\eta^2 = 0.163$), but no such effects on the later 11–15 Hz alpha windows. Follow-up testing revealed that alpha oscillations were weaker (i.e., less negative relative to baseline) in the left inferior frontal gyrus following left DLPFC-occipital stimulation relative to both right-occipital stimulation (95 % CI [.134, .805], $p = .006$) and sham (95 % CI [.221, .907], $p = .001$; Fig. 5). Significant stimulation effects were also found on the gamma responses (52–74 Hz, 2.3–2.5 s) in the right lateral occipital cortices ($F[2,76] = 12.716$, $p < .001$, corrected, $\eta^2 = 0.251$). Post hoc testing showed that left DLPFC-occipital stimulation induced stronger gamma oscillations compared to both right DLPFC-occipital

stimulation (95 % CI [.395, 1.108], $p < .001$) and sham (95 % CI [.210, .884], $p = .001$; Fig. 5) conditions.

4. Discussion

A growing body of research has examined the effects of neuro-stimulation over the prefrontal cortices on WM function. However, modulatory effects have generally been modest, with considerable variability in results across studies, although at least some of this variability is attributable to differences in study design (e.g., different stimulation montages, duration and amplitude of stimulation, etc.). Herein, we investigated the impact of network-level stimulation using a novel dual-montage HD-tDCS configuration targeting the left DLPFC-occipital and right DLPFC-occipital sites, and evaluated changes in whole-brain neural dynamics during a verbal WM task using MEG in healthy adults. Our findings reveal significant, montage-specific effects on neural oscillatory responses during different phases of verbal WM processing. Specifically, left DLPFC-occipital stimulation tended to modulate domain-specific neural activity during encoding, while both active stimulation conditions affected broader WM networks. Below, we discuss the implications of these findings.

Our most interesting findings were the montage-specific modulatory effects on encoding and maintenance responses. During encoding, left DLPFC-occipital stimulation elicited stronger theta activity in the left STG relative to right DLPFC-occipital stimulation and sham. The left STG is a critical hub for language processing, with known roles in phonological decoding and temporary phonological code storage (Graves et al., 2008; Simos et al., 2000, 2002; Wilson et al., 2005b, 2005a, 2007). The observed enhancement of theta oscillations may reflect increased engagement of phonological loop resources, supporting the rehearsal of verbal information during early encoding. Additionally, both left and right DLPFC-occipital stimulation induced stronger theta oscillations in the left supramarginal and angular gyri compared to the sham. These regions are central to the language processing network and have been widely reported in neuroimaging studies of verbal WM (Arif et al., 2024; Embury et al., 2019; Heinrichs-Graham and Wilson, 2015; Koshy et al., 2020; Pavlov and Kotchoubey, 2022; A.L. Proskovec et al., 2019; Wiesman et al., 2021; Wilson et al., 2017). Theta activity in these areas has been strongly linked to attentional processes, with increased theta power reflecting heightened cognitive control and task engagement, and such increases are likely a result of increased top-down control (Fernández et al., 2021; Jensen and Tesche, 2002; Maurer et al., 2015; Spooner, Eastman, et al., 2020, 2020). Notably, a prior tDCS study examining left vs right DLPFC stimulation on neural responses during a verbal WM task did not report theta modulation (Koshy et al., 2020). In contrast, the dual-montage tDCS approach applied in this study revealed modulation of theta across distributed WM networks, suggesting that DLPFC-occipital stimulation may modulate both spectrally-specific local activity and more distant responses relative to what has been reported with single-site montages. However, caution is warranted as our study was not designed to compare the effect of dual-montage tDCS with single region tDCS. Thus, we are unable to directly evaluate the superiority of the modulatory effect elicited by each approach. Future studies should employ each approach to more precisely delineate the potential effects of network level compared to single montage DLPFC-occipital stimulation, which will help optimize stimulation montage designs to maximize neural excitability.

Interestingly, right DLPFC-occipital stimulation resulted in attenuated cortical activation, as indexed by increased alpha power relative to baseline, in the right superior parietal cortex during late encoding relative to both left DLPFC-occipital stimulation and sham. The superior parietal cortex, a critical hub in both the dorsal attention network and dorsal visual stream, receives extensive feedback and feedforward projections from frontal and occipital regions (Corbetta and Shulman, 2002). Thus, the observed suppression of alpha activity may reflect inhibitory mechanisms that enhance verbal task engagement by disengaging neural resources in region more specialized for spatial processing (Foxy and Snyder, 2011; Jensen, 2024; Sauseng et al., 2005). This aligns with prior work implicating the right DLPFC in spatial aspects of WM (Curtis et al., 2004; Curtis and D'Esposito, 2003; Giglia et al., 2014; A.L. Proskovec et al., 2018; A.L. 2019; Wu et al., 2014). Our finding of weaker alpha responses in the left superior parietal following right DLPFC-occipital stimulation compared to sham, but not left DLPFC-occipital stimulation, may suggest shared and functionally distinct processes between hemisphere during verbal WM. Previous literature has shown that bilateral parietal cortices contribute to attentional demands and WM, as well as hemispheric specialization for verbal (left parietal) and spatial (right parietal) processes (Nagel et al., 2013; Schach et al., 2023). Importantly, one recent study found a dissociation between activation in the left versus right parietal cortices during WM performance, with decreased activity in the left parietal cortices likely reflecting higher WM capacity (Kiyonaga et al., 2021). As such, modulation of the right DLPFC may result in decreased utilization of left hemispheric resources during the encoding process. In addition to the hemispheric specificity of stimulation effects in the superior parietal cortices, both active stimulation conditions induced weaker alpha activity in the right IFG and right cerebellum compared to sham. Emerging evidence suggests that the dorsal cerebellum contributes to phonological WM, extending beyond its classical role in motor control (Brissenden and Somers, 2019; Kirschen et al., 2005). The reduced alpha activity in these regions may indicate more efficient encoding, requiring fewer neural resources without behavioral performance trade-offs. This aligns with prior findings showing inhibitory projections from the cerebellum to the inferior frontal cortices and their involvement in cognitive control processes (Okayasu et al., 2023).

The effects of left DLPFC-occipital stimulation extended into the early maintenance phase, where we observed weaker alpha oscillations (i.e., less negative relative to baseline) in the left IFG following left relative to right DLPFC-occipital stimulation and sham. This finding likely reflects the left-lateralized engagement of the IFG in verbal and rule-based cognitive processes (Goldberg et al., 1994; Nagel et al., 2013). The observed weaker alpha activity may suggest that left DLPFC-occipital stimulation enhances local processing, potentially through inhibitory mechanisms that help suppress interference from task irrelevant cortical processing occurring in other brain regions. These results are consistent with models positing that increases in alpha power functions as a gating mechanism to facilitate WM maintenance (Bonnefond and Jensen, 2012; Jensen and Mazaheri, 2010; A.L. Proskovec et al., 2019; Sauseng et al., 2005). Additionally, left DLPFC-occipital stimulation increased gamma activity in the lateral occipital cortex during maintenance. This may reflect recurrent processing between occipital and higher-order brain regions, mediated by top-down feedback from the prefrontal cortices to support sustained neural

representations (e.g., persistent firing). This interpretation is supported by primate studies showing that gamma band oscillations can carry and maintain visual features via multiple transient bursts (Lundqvist et al., 2016; M. 2018; Tallon-Baudry et al., 1999; Tallon-Baudry and Bertrand, 1999), as well as human studies linking stronger gamma power during maintenance to improved WM retrieval (Jokisch and Jensen, 2007; Tallon-Baudry et al., 1998). These findings align with the most widely theorized neurophysiological effects of tDCS, mainly that it modulates cortical excitability by influencing both excitatory glutamatergic and inhibitory GABAergic neurotransmission (Bachtiar et al., 2015; Bunai et al., 2021; Stagg et al., 2009, 2011). Anodal stimulation has been associated with reduced GABA concentrations in targeted local brain regions, potentially facilitating neural disinhibition and plasticity (Bachtiar et al., 2015; V. 2018; Kim et al., 2014). However, these interpretations remain speculative and require validation to quantify region-specific neurometabolic changes, including high-field magnetic resonance spectroscopy (MRS) work using targeted sequences. Of note, a recent tDCS-MRS study found increased Glx levels (i. e., a combined measure of glutamate and glutamine) in the left DLPFC following stimulation, with no significant changes in GABA (Vural et al., 2024). Future research leveraging the focality of HD-tDCS could further delineate these neuromodulatory effects.

Despite the novel neural findings presented here, several limitations warrant consideration. First, we did not measure WM performance or MEG responses prior to each stimulation session, and thus there could have been baseline differences on any given day. Our rationale for not collecting such measures was that studies have shown that MEG maps are stable in the same participant over many months, with some variation based on the time of day of the recording (Lew et al., 2021; McCusker et al., 2021; Wilson et al., 2014). Thus, we controlled for this by scheduling each participant's three appointments at the same time of day. While there could still be some day-to-day variability (e.g., a person slept poorly the night before), this was unlikely to systematically vary with tDCS condition across our sample. Second, we observed no significant behavioral effects, a common finding in tDCS studies involving healthy participants. This may be attributable to insufficient stimulation intensity, non-optimal montage configuration, or task parameters, or more simply that healthy young adults can often compensate for temporary changes in arousal and other factors that affect performance. Task difficulty and baseline WM capacity have also been identified as factors that modulate the effectiveness of stimulation in affecting behavior, where increased task difficulty may enhance the interaction effect with stimulation on performance outcomes (Hill et al., 2018). Future work should consider using more strenuous WM paradigms, including those with higher WM loads (A.L. Proskovec et al., 2019). Nevertheless, despite the null findings on behavioral outcomes in the current study, our results showing robust neurophysiological effects in the context of dual-montage stimulation contribute significantly to our understanding of current mechanistic foundations used to explain the effects of tDCS on the neural dynamics underlying verbal WM (Reinhart et al., 2017). Lastly, we used only a dual-montage design and implementing one or more single region montages as a separate condition in the same experiment would enable stronger conclusions. While increasing the number of stimulation sites and/or montage conditions prolongs the setup and leads to greater participant fatigue, the benefits may outweigh the costs in many scenarios.

En masse, this is the first study to employ a dual-montage DLPFC-occipital HD-tDCS design to investigate the effects of stimulation on the neural dynamics underlying verbal WM. Future studies should examine whole-brain connectivity to better characterize network-level modulatory effects and consider frequency-specific interventions such as transcranial alternating current stimulation (tACS) or temporal interference (TI) stimulation to further refine mechanistic insights (Spooner and Wilson, 2023). Overall, continued research is essential to optimize tDCS montages for potential clinical applications.

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Data availability

The data used in this article will be made publicly available through the COINS framework at the completion of the study (<https://coins.trendscenter.org/>).

Data will be made available on request.

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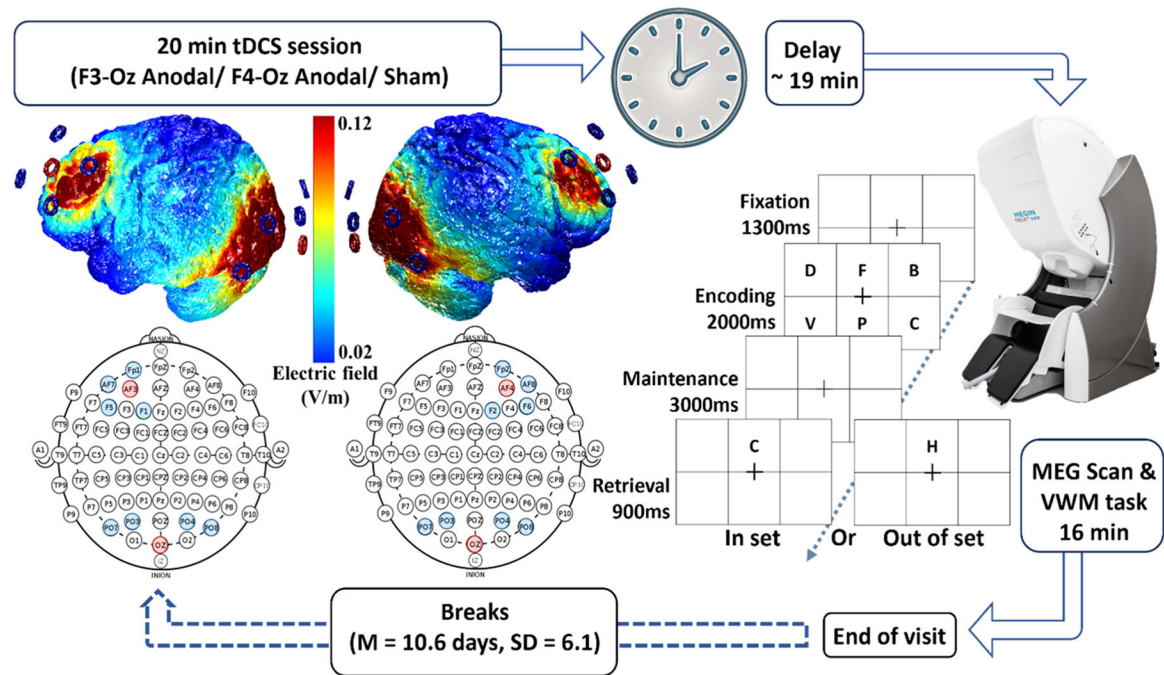


Fig. 1. HD-tDCS current flow modeling, task paradigm, and study timeline.

Current flow modeling revealed relatively focal stimulation over the prefrontal and occipital cortices. Participants received 20 min of anodal HD-tDCS using a dual-montage design (i.e., left DLPFC – occipital, right DLPFC – occipital, sham) that was administered across three visits separated by about a week ($M = 10.6$ days) using a pseudorandomized cross-over design. After stimulation, participants completed a verbal WM task during MEG. Briefly, a fixation cross embedded within an empty 2×3 grid was presented on the screen, followed by six consonants for 2 s (encoding). The six consonants then disappeared for 3 s (maintenance) and a single probe letter appeared in the upper middle box of the grid for 0.9 s (retrieval). Participants were asked to respond as to whether the probe was among the six consonants presented during the encoding grid.

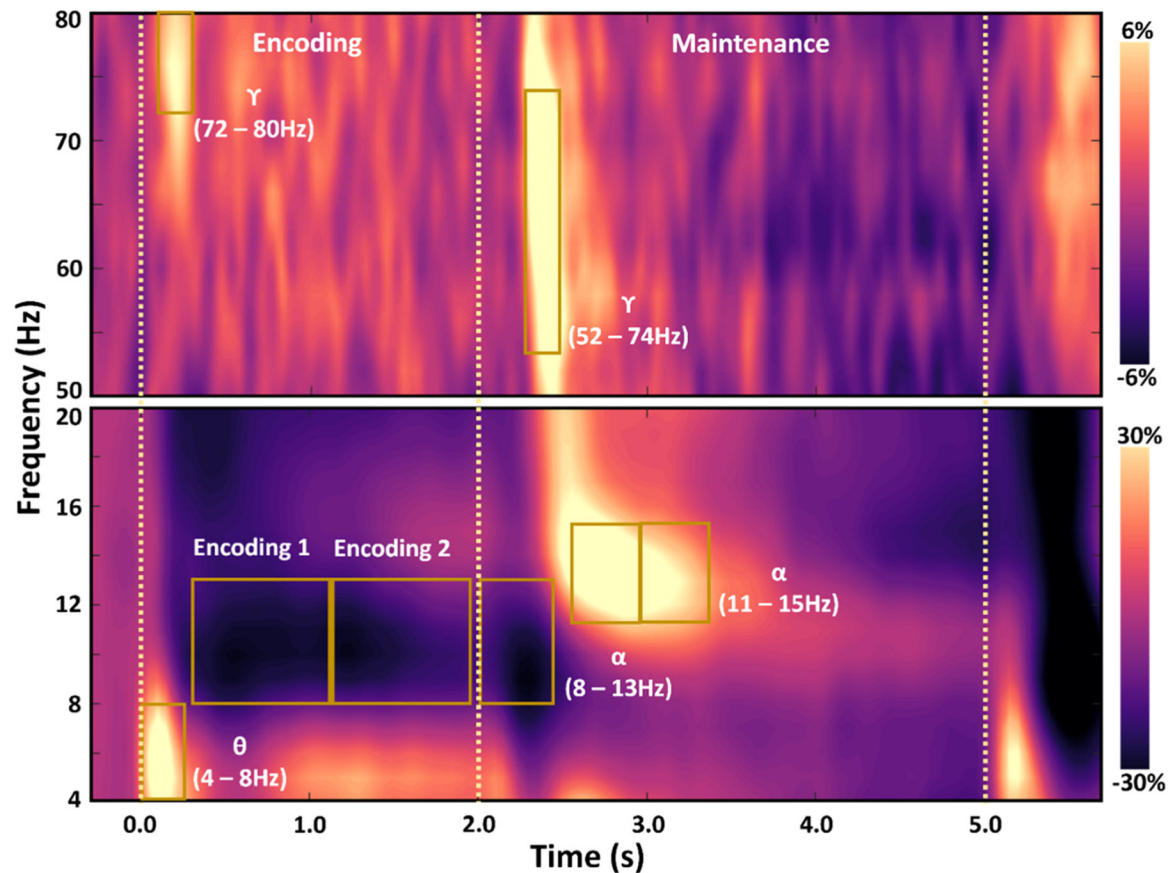


Fig. 2. Time-frequency spectrograms during the verbal working memory task.

Grand-averaged time-frequency spectrograms of MEG sensors exhibiting one or more significant oscillatory responses, with gamma activity at the top and theta and alpha activity at the bottom. All signal power data are expressed as percent differences from baseline, with the scale bars shown on the far right for each spectrogram. The boxes indicate the time-frequency windows that were significantly different from baseline and thus used for beamforming. The dotted vertical lines indicate the onset of the encoding grid (0.0 s), as well as the beginning (2.0 s) and end (5.0 s) of the maintenance period. Note that significant responses can also be seen during the retrieval period, but these responses were not examined due to the planned task differences between in-set and out-of-set trials.

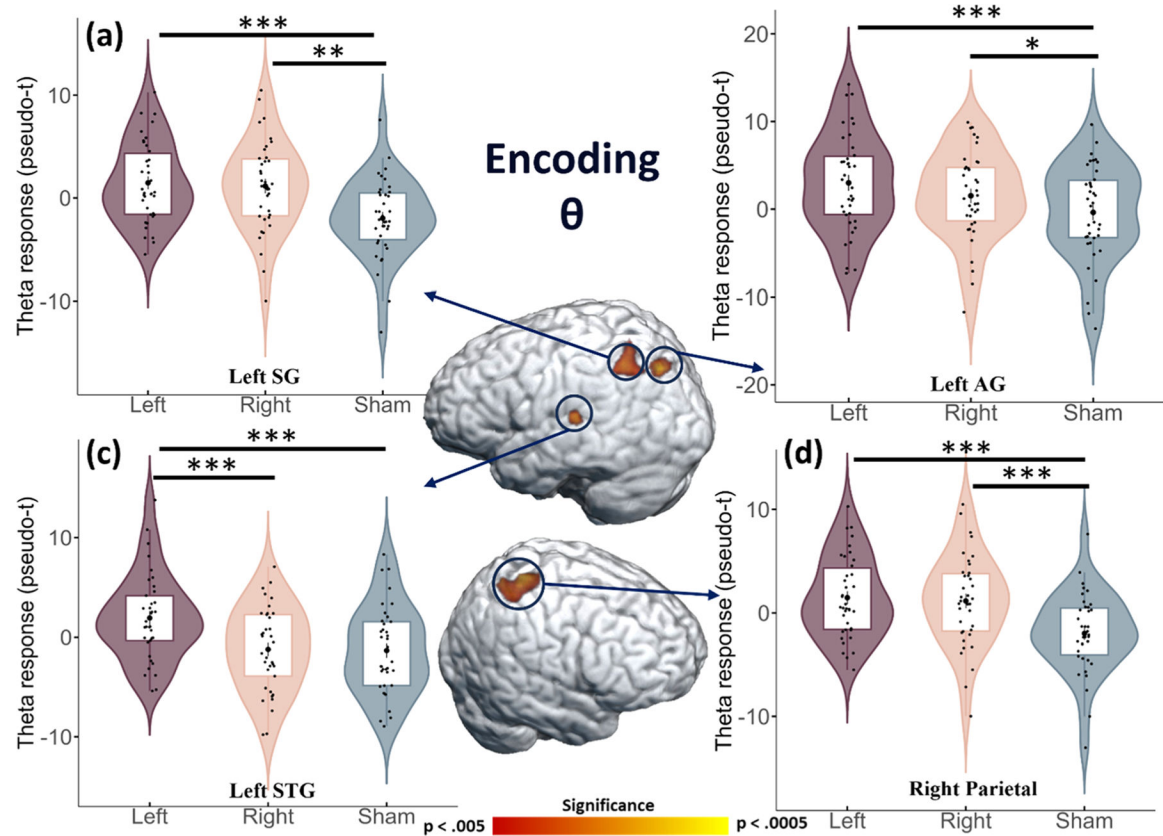


Fig. 3. HD-tDCS effects on theta oscillations during encoding.

Whole-brain 1×3 RM-ANOVAs were performed to examine significant stimulation effects on theta activity during encoding. Significant effects were found in the (a) left supramarginal gyrus, (b) left angular gyrus, (c) left superior temporal gyrus, and (d) right parietal cortices. Post hoc testing revealed stronger theta responses in the left supramarginal gyrus, left angular gyrus, and the right parietal cortices following both left and right DLPFC-occipital stimulation compared to sham. Left DLPFC-occipital stimulation also induced stronger theta responses in the left superior temporal gyrus compared to both right DLPFC-occipital stimulation and sham. Note that the red-yellow color scheme in the brain maps reflect increases in theta power (i.e. increased neural activity). SG: supramarginal gyrus (SG); AG: angular gyrus; STG: superior temporal gyrus. $*p < .05$, $**p < .005$, $***p < .001$.

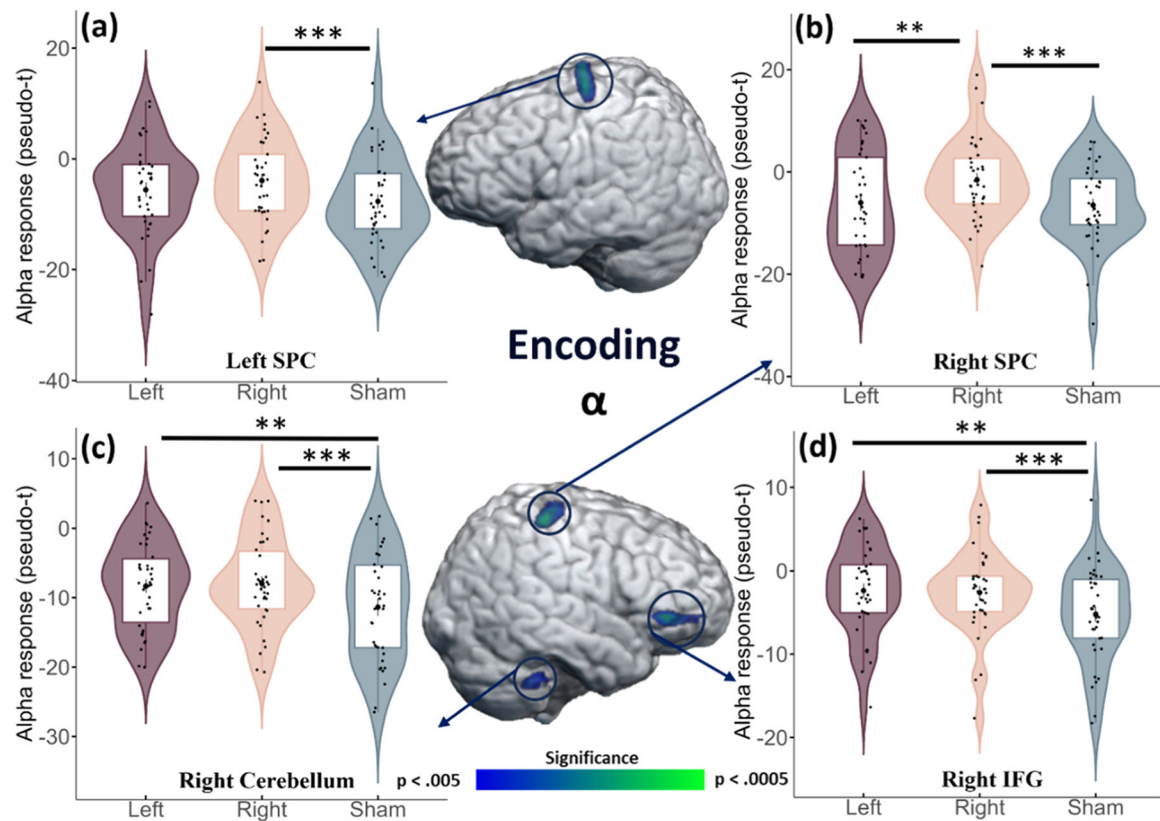


Fig. 4. HD-tDCS effects on alpha oscillations during late encoding.

Whole brain 1×3 RM-ANOVAs were performed to examine stimulation effects on alpha activity during the encoding period. Significant effects were found in the (a, b) bilateral superior parietal, (c) right cerebellum, and (d) right inferior frontal gyrus. Post hoc testing revealed weaker alpha responses (i.e., less negative relative to baseline) in the right cerebellum and the right inferior frontal cortices following both left and right active stimulation compared to sham, while right DLPFC-occipital stimulation induced weaker alpha oscillations in the bilateral superior parietal cortices relative to sham, as well as weaker alpha responses relative to left DLPFC-occipital stimulation in the right parietal cortices. Note that the blue-green color scheme used in the brain maps reflects weaker alpha power (i.e., more negative relative to baseline). SPC: Superior parietal cortices; IFG: Inferior frontal gyrus. $**p < .005$, $***p < .001$.

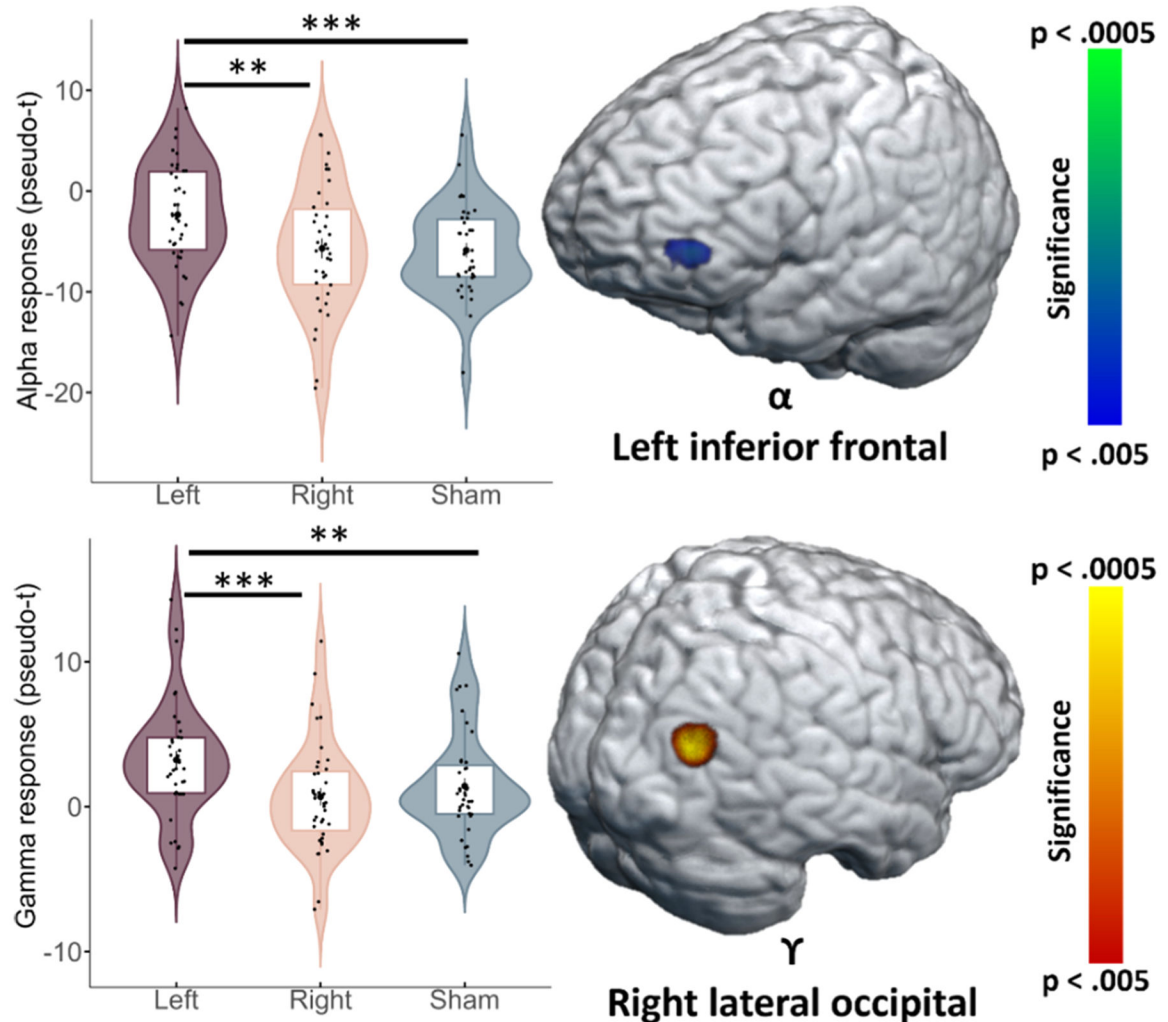


Fig. 5. HD-tDCS effects on maintenance related neural oscillatory activity.

Whole brain 1×3 RM-ANOVAs were used to examine stimulation effects on alpha and gamma activity during the memory maintenance period. Significant effects were found in the (a) left IFG for alpha oscillations and the (b) right lateral occipital cortices for gamma activity. Post hoc testing revealed weaker alpha responses in the left IFG following left DLPFC-occipital stimulation relative to both right DLPFC-occipital stimulation and sham. For gamma responses, left DLPFC-occipital stimulation induced stronger oscillations in the right lateral occipital cortices relative to both right DLPFC-occipital stimulation and sham. The blue-green color scheme in the top brain map represents weaker alpha power (i.e., more negative relative to baseline), while the red-yellow color schemes in the bottom brain reflects increased gamma power (i.e., stronger neural activity). IFG: Inferior frontal gyrus; LOC: Lateral occipital cortices. ** $p < .005$, *** $p < .001$.