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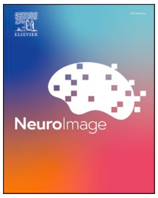

Bifocal alpha-band tACS modulates temporal sampling in visual perception

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ABSTRACT

Alpha oscillations (7–13 Hz) have been historically considered to shape temporal sampling processes in the visual modality, with faster alpha frequencies linked to finer temporal resolution. However, evidence is mostly correlational, and findings are not always replicated. Here, we investigated the role of alpha oscillations in temporal sampling using transcranial alternating current stimulation (tACS) and electroencephalography (EEG). Over three consecutive blocks, bilateral high-definition tACS was applied over extra-striate visual areas including V5/MT at either the individual alpha frequency (IAF), IAF+2, or IAF-2 Hz while participants performed a two flash fusion task. In line with previous findings, baseline resting-state IAF correlated with temporal segregation accuracy, with higher IAF predicting better segregation ability. Importantly, stimulation at IAF+2 Hz improved temporal segregation accuracy, whereas IAF-2 Hz decreased performance. This effect was specific for stimuli in the right hemifield, highlighting important hemispheric differences in alpha-mediated visual temporal sampling. Following stimulation, EEG data revealed no shift in the IAF and a decrease of alpha power independently from stimulation condition. Nonetheless, specifically for the IAF+2 stimulation, we observed a modulation of the aperiodic exponent of the power spectrum, indicating possible changes in cortical excitability as a short-term plasticity mechanism that persists beyond online tACS effects. Taken together, these results corroborate the role of alpha oscillations in defining temporal sampling processes and add novel evidence on the neurophysiological effects of tACS.

1. Introduction

Temporal processing is a crucial aspect of the visual system. On one hand, segregation mechanisms define the temporal resolution of perception, whereas integration mechanisms enable a coherent and seemingly continuous perception of events and objects. It has been suggested that temporal segregation and integration processes synergically contribute to the temporal sampling of the continuous stream of visual information (VanRullen, 2016; Varela et al., 1981). Temporal sampling varies across different timescales based on task demands (Melcher et al., 2014; Ronconi et al., 2017; Ronconi et al. 2024; Ronconi and Bellacosa Marotti, 2017; Wutz et al., 2016), and interindividual differences (Donohue et al., 2010; He et al., 2020; Lee and Noppeney, 2014; Saija et al., 2019). Furthermore, numerous studies documented altered temporal segregation/integration processes across and within sensory modalities in several neurodevelopmental and psychiatric conditions (e.g., Freschl et al., 2021; Haß et al., 2017; Marsicano et al., 2022; Ronconi et al., 2020; 2023; Santoni et al., 2025; Zhou et al., 2020; Cavicchioli et al., 2024).

Growing evidence has suggested that temporal processing operates in a cyclical manner, with visual inputs being rhythmically sampled from the environment as neuronal activity alternates between excitation and inhibition (Busch et al., 2009; Mathewson et al., 2009; VanRullen, 2016). Following seminal works in the mid-20th century (Coffin and Ganz, 1977; Kristofferson, 1967a, 1967b), an increasing amount of evidence from human magneto- and electro- encephalography has linked alpha oscillations (~7–13 Hz) to visual temporal sampling, indicating that a higher temporal resolution is associated with faster resting-state alpha rhythms (for a recent review and meta-analysis see: Samaha and Romei, 2024). Further evidence has shown that changes in the ongoing

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alpha frequency prior to stimulus presentation predict temporal processing accuracy in a trial-by-trial manner and are linked to task demands (Drewes et al., 2022; Ronconi et al., 2017; Ronconi et al., 2024; Samaha and Postle, 2015; Wutz et al., 2016).

Starting from correlational findings, recent studies have investigated the possibility of enhancing temporal sampling mechanisms by using modulatory techniques designed to alter the speed of ongoing oscillations. In this direction, sensory entrainment studies have demonstrated that it is possible to modulate temporal sampling by delivering rhythmic sensory stimulation at different alpha frequencies prior to target onset (Marsicano et al., 2024; Ronconi et al., 2018). Another promising tool to investigate temporal sampling is transcranial Alternating Current Stimulation (tACS), a non-invasive electrical stimulation technique that delivers sinusoidal currents at specific frequencies over the scalp. Studies employing tACS have demonstrated the feasibility of modulating perceptual and attentional processes within and across the senses, by delivering electrical currents individually tailored to endogenous alpha rhythms (Battaglini et al., 2020; Cecere et al., 2015; Kemmerer et al., 2022; Minami and Amano, 2017; Mioni et al., 2020; for a review see Ghiani et al., 2021).

Despite these promising results, there is still no evidence directly linking temporal sampling in the visual system to neurophysiological modulations induced by tACS. According to the entrainment account, tACS is thought to synchronize endogenous oscillations to an external driving force (i.e., the stimulation frequency), resulting in a power enhancement at the stimulated frequency (Ali et al., 2013; Fröhlich and McCormick, 2010; Thut et al., 2011; Vogeti et al., 2022). An alternative account of tACS aftereffects is Spike-Timing-Dependent Plasticity (STDP), according to which synaptic changes are influenced by the timing of neuronal firing within the target neural network (Vogeti et al., 2022). Specifically, it has been hypothesized that when the frequency of tACS is lower than the natural frequency of the stimulated network the pre-synaptic potentials temporally precede post-synaptic potentials, leading to long term potentiation, while the opposite occurs when the stimulation frequency is higher (Veniero et al., 2015; Vossen et al., 2015; Wischnewski and Schutter, 2017; Zaehle et al., 2010).

While immediate effects consistent with the entrainment hypothesis have been observed in vitro and in animal models (for reviews, see Balieva et al., 2021; Liu et al., 2018), there is limited evidence of entrainment-related effects in humans following tACS (reviewed in Millard et al., 2024). This is partly due to the technical challenges of analyzing EEG data contaminated by tACS-induced electrical artifacts, which is why offline EEG recordings are often used to capture more stable, artifacts-free and longer-lasting effects. Recent studies have explored the possibility that longer-lasting plastic changes driven by tACS and observed offline might be better captured by broadband modulations of the power spectrum underlying excitation/inhibition changes of neuronal firing (Masina et al., 2025).

The aim of the present study is to investigate visual temporal sampling and its neural correlates using a neuromodulatory approach. Specifically, we aim to determine whether bilateral high-definition (HD) tACS delivered over parieto-occipital cortices at the IAF or at off-peak alpha frequencies (IAF+2 Hz, IAF-2 Hz) can result in the modulation of temporal sampling mechanisms within a 2 Flash Fusion Task (2FFT). We expect to find an increased temporal resolution when tACS is delivered at higher alpha frequencies (IAF+2 Hz) and a reduced performance when tACS is delivered at lower alpha frequencies (IAF-2 Hz). This hypothesis is based on previous correlational findings showing that the temporal segregation of rapidly presented flashes improves as a function of the IAF (Samaha and Romei, 2024). Similarly, the selection of the stimulation electrodes (PO7-PO8) is based on a previous tACS montage that proved to be effective in modulating behavioral performance within a 2FFT when stimulating at alpha frequencies (Battaglini et al., 2020). This stimulation configuration creates a focal electrical field distribution targeting extra-striate visual regions including the areas V5/MT of both hemispheres, which are well known for their involvement in visual timing processes (Battaglini et al., 2020; Battelli et al., 2007; Bueti et al., 2008a,b; Salvioni et al., 2013). Supporting this choice, a recent MEG study by Ronconi et al. (2024) demonstrated that performance in the same 2FFT paradigm could be decoded from neural activity in V5/MT, further confirming the relevance of this area in visual temporal integration/segregation processes.

To prove the neurophysiological correlates of these behavioral effects, we analyze a range of EEG outcomes. Specifically, we investigate changes in both the oscillatory (IAF and alpha power) and aperiodic components (slope and offset) of the power spectrum in resting-state EEG data recorded immediately before and after stimulation.

While the analysis of oscillatory activity is directly motivated by the proposed mechanisms of tACS, our investigation of aperiodic activity is exploratory. In recent years, there has been growing recognition of the importance of separating oscillatory (periodic) signals from the aperiodic background activity in EEG (Donoghue et al., 2020). Specifically, the aperiodic activity of the power spectrum is characterized by the exponent, the χ parameter of the $1/f^{\chi}$ function describing the power spectrum, and the offset, the broadband power across frequencies (Donoghue et al., 2020). While the offset has been linked to population spiking activity, the aperiodic exponent is thought to reflect neurophysiological changes in the excitation/inhibition (E/I) balance (Gao et al., 2017; Voytek and Knight, 2015). Recent tACS studies have reported offline modulations of these aperiodic components (Di Dona et al., 2024; Davis et al., 2023; Kasten et al., 2024; Masina et al., 2025), suggesting that non-rhythmic broadband changes may also contribute to post-stimulation effects. Including these measures allows us to test whether broader changes in neural excitability, not only frequency-specific effects, could play a role in shaping temporal processing. In line with this idea, recent experimental evidence has also suggested that aperiodic activity can be modulated in relation to perceptual processes, alongside with oscillatory activity (Cunningham et al., 2023; Deodato and Melcher, 2024; Krystecka et al., 2024; Santoni et al., 2025; Turri et al., 2023). Although speculative, this framework offers a complementary route to understanding the broader neurophysiological effects of alpha-frequency tACS. Taken together, this study aims to elucidate the relationship between alpha-band oscillations and visual temporal sampling by employing HD-tACS to modulate these rhythms and examining the resulting online behavioral effects and offline neurophysiological short-term plastic changes.

2. Methods

2.1. Participants

A total of 32 participants participated in the study after signing informed consent. From the initial sample size, two participants were excluded either for faulty EEG recording or because of low accuracy at the task (one subject was removed because of a mean accuracy of 0.03), resulting in a final sample size of 30 participants (14 males, 16 females, mean age = 24 years, range: 20–29 years). They all had normal or corrected-to-normal vision and no history of psychiatric or neurological disorders. The majority of participants were university students (mean years of education = 17, range: 14–21 years). Participants were naive to the purpose and design of the study and met the criteria for the application of tACS (Antal et al., 2017). The study was approved by the Ethics Committee of the Department of General Psychology of the University of Padova (protocol number 5034).

2.2. Stimuli and procedure

During the task, participants were positioned at a distance of 90 cm from the monitor using a chinrest. All stimuli were presented on a light-gray background of a 24.5-inch monitor with a 1920 × 1080 resolution screen and a refresh rate of 100 Hz. Stimuli were presented using Psychotoolbox v. 3.0.18 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) for MATLAB R2021b for Windows (The MathWorks Inc., 2021) and consisted of Gaussian blobs (hereafter referred to as "flashes") sized 0.5° × 0.5°. Each trial began with a fixation point at the center of the screen lasting for a jittered duration of 500 ms (jitter = ± 500 ms), which participants were asked to fixate for the duration of the trial. Following, one or two flashes could appear randomly either on the left or on the right side of the fixation point with a stimulus offset of 7° from center of the screen. The two flashes lasted 10 ms each and were intervalled by an Interstimulus Interval (ISI) of varying duration (10, 20, 30, 40, 50, 60, 70 ms). 20 % of the trials consisted of catch trials, where only one flash was presented for a total duration of 20 ms, equating the duration of two flashes. Participants were asked to detect the presence of one vs. two flashes and to respond with the corresponding key on a keyboard (Fig. 1B). The experimental procedure, outlined in Fig. 1A, involved each participant in three separate blocks of the 2FFT, during which they received tACS at three different stimulation frequencies (IAF, IAF+2 Hz, IAF-2 Hz). Block order was counterbalanced across participants using a Latin square design to minimize order effects. Off-peak frequencies were set to ± 2 Hz with respect to IAF in accordance with prior tACS literature demonstrating frequency-specific behavioral effects (Cecere et al., 2015; Kemmerer et al., 2022; Mioni et al., 2020; Ronconi et al., 2020), as well as with evidence showing modulation of visual temporal resolution using sensory entrainment at comparable frequency shifts (Marsicano et al., 2024; Ronconi et al., 2018). Each block lasted 15 min, resulting in an average total number of 1233 trials (SD = 107) per participant. Before and after each of the three blocks, we acquired eyes-closed, resting state EEG data for 4 min. All blocks occurred on the same day at a distance of 40 min. This washout period was set in accordance with prior literature in order to minimize fatigue and potential tACS after-effects (Cecere et al., 2015; Mioni et al., 2020). At the end of the experimental procedure, participants filled a questionnaire (Fertonani et al., 2015) to evaluate their sensations during the stimulation (see Supplementary Materials).

2.3. Stimulation settings and EEG recording

tACS stimulation was administered using a StarStim32 device, a hybrid neurostimulation system for concurrent EEG/tACS, managed through the software Neuroelectrics Instrument Controller (NIC 2.0). We employed 9 PISTIM Ag/AgCl electrodes for both stimulation and EEG recording purposes, along with 23 GELTRODE Ag/AgCl electrodes solely for EEG recording. The electrodes had a radius of 1 cm and were positioned according to the 10–10 system configuration. EEG recordings were acquired with a sampling rate of 500 Hz, with the right earlobe as online reference. For stimulation electrodes, impedance was kept below 10 kΩ. For EEG electrodes, the Quality Index computed by NIC2 software was kept between 0 and 0.5 (highest rank). This index depends on line noise power at 50 Hz (μV^2), main noise power of the standard EEG 1–40 Hz band (μV^2), offset (mean value of the waveform).

Stimulation electrodes were placed at PO8 and PO7; return electrodes were Oz, P3, P4, PO9, PO10, TP7 and TP8 (Fig. 1C). Stimulation intensity was set to 0.8 mA for each stimulation electrode, with an offset at 0 mA (resulting in a peak-to-peak intensity of 1.6 mA), in accordance with safety guidelines (Antal et al., 2017), as well as previous studies that showed behavioral modulations using same intensity at similar HD-montages (Battaglini et al., 2020; Di Dona et al., 2024). Simulations conducted using SimNIBS 2.1 (Saturnino et al., 2019) confirmed that the peak electric field strength at the bilateral parieto-occipital targets (PO7/PO8) reached approximately 0.13 V/m (Fig. 1C), which is in line with previous work showing behavioral modulations following HD-tACS (Battaglini et al., 2020; Di Dona et al., 2024; Kemmerer et al., 2022). Each stimulation session started with a ramp-up phase of 20 s, with the electrical current gradually increasing from 0 to ± 0.8 mA. Full stimulation intensity was maintained for 15 min, during which participants were engaged with the 2FFT. Following, stimulation current was gradually reduced back to 0 mA during a ramp-down phase of 20 s. Stimulation frequency was individualized based on the IAF, estimated for each participant from the first resting state EEG recording. To find the alpha peak in the power spectrum, we filtered the raw EEG data with a bandpass filter (cutoff: 0.05 - 40 Hz) and a notch filter at 50 Hz using the EEGLAB 2021.1 toolbox (Delorme and Makeig, 2004) for MATLAB (The MathWorks Inc., 2021). Following, we computed the fast Fourier transform (FFT) power spectrum between 1 and 30 Hz by multiplying epoched data (epoch length: 1 s) to a Hanning taper, zero padded to a length of 2 s, using FieldTrip toolbox version 20.230.118 (Oostenveld et al., 2011). The IAF peak was computed as the local maximal power in the frequency band between 7 and 13 Hz, considering the average frequency between the two stimulation electrodes (PO7 and PO8), with a frequency resolution of 0.25 Hz.

2.4. Behavioral data analysis

Data from the 2FFT were analyzed using two generalized linear mixed-effects models (GLMM) with a logit link-function using the package lme4 in R (Bates et al., 2015). In the first model, we aimed at predicting accuracy for the perception of two flashes using the following formula: $\textit{2 flash accuracy} \sim \textit{Condition} * \textit{ISI} * \textit{Hemifield} + \textit{resting-state IAF} + (1|\textit{ID})$. The model included the categorical predictors Condition (IAF,

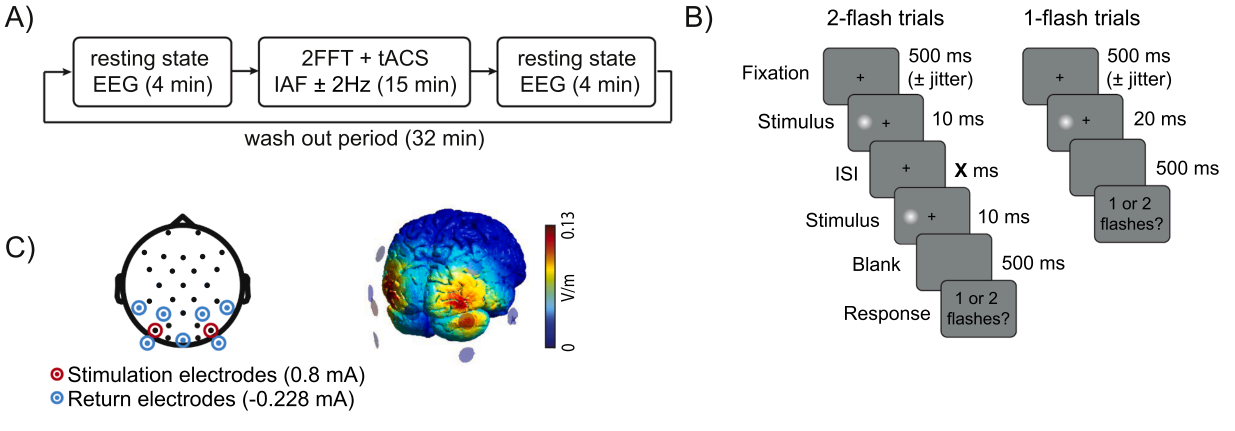

Fig. 1. A) Schematic representation of the experimental design. The procedure was repeated 3 times for each participant, counterbalancing the order of the stimulation frequency (IAF, IAF+2 Hz, IAF-2 Hz); B) Outline of a trial for the 2 Flash Fusion Task: one or two flashes are presented in rapid succession in either the left or the right hemifield, separated by an Interstimulus Interval of varying duration. Participants were instructed to report whether they perceived one or two flashes; C) tACS/EEG montage (left) and the estimated electric field distribution on the cortical surface (right). 2FFT = 2 Flash Fusion Task, IAF = Individual Alpha Frequency, ISI = Interstimulus Interval.

IAF+2 Hz, IAF-2 Hz) and Hemifield (Left, Right), and the continuous predictors of ISI (from 0 to 70 in steps of 10 ms) and resting-state IAF after being scaled. For each participant we included the IAF computed from the first resting-state recording, before any stimulation. A second model was run for predicting accuracy for the perception of single flash trials using the following formula: *1 flash accuracy* ~ *Condition* * *Hemifield* + *resting-state IAF* + *(1|ID)*. The second model was conducted as a control analysis to determine whether the effects observed in the first model were specific to 2-flash perception (i.e., temporal segregation) or if they were related to broader perceptual effects. Note that when continuous covariates are added, the effects are estimated over the mean value of the covariates. The models included all the fixed factors described above as well as all their possible interactions. Participant ID was included as a random intercept. Chi-square tests were conducted on all fixed effects and interactions using the 'Anova' function from the package car in R (Fox and Weisberg, 2019). Post-hoc comparisons were implemented via the package emmeans in R (Lenth et al., 2018) on the estimated marginal means (EMMs) of the model. P-values were corrected using the False Discovery Rate (FDR) correction for multiple comparisons (Benjamini and Hochberg, 1995).

2.5. EEG data analysis

Although the setup allowed for simultaneous EEG and stimulation, EEG data recorded during stimulation were not analyzed. Only resting-state EEG collected immediately before and after each stimulation block was used in the current analyses. Resting state EEG data were preprocessed offline using EEGLAB 2021.1 toolbox in MATLAB (Delorme and Makeig, 2004). Raw data were re-referenced to an average reference and filtered using a Butterworth filter of second order with cutoff frequencies at 0.05–80 Hz and a notch filter at 50 Hz. The continuous resting-state EEG data were divided into 1-second-long epochs. We performed spherical interpolation to channels with a voltage higher than a set threshold around ±150 μV for >30 % of the total epochs, leading to the interpolation of an average of 0.08 channels (0.34 SD). Following, we performed an Independent Component Analysis (ICA) to detect Independent Components related to eye and muscle artifacts. We removed components that were classified by the ICLabel algorithm as "eye" or "muscle" artifacts with a probability >90 % (mean number of removed components = 0.13, 0.41 SD). Finally, we rejected epochs with a voltage higher than ±150 μV for >30 % of the total epochs, resulting in an average of 9.33 % (1.19 SD) removed epochs.

In order to investigate spectral differences, resting-state EEG data were multiplied to a Hanning taper, zero padded and fast Fourier transformed with a frequency resolution of 0.25 Hz across the frequency range between 1–40 Hz. Following, we employed the "specparam" algorithm to parametrize the periodic and aperiodic components of the power spectrum (Donoghue et al., 2020). This approach models the aperiodic component of the power spectrum by applying a Lorentzian function and the periodic component by fitting a Gaussian function to each oscillatory peak (Donoghue et al., 2020). For peak fitting, the following parameters were used: minimum peak height = 0.001, maximum number of peaks = 3, peak threshold = 0.5, proximity threshold = 2, peak width limits = 0.5–12, aperiodic mode = "fixed". These settings resulted in model fits with a mean R^2 of 0.98 and a mean error of 0.01. The following indices were computed for each electrode: i) the IAF, the frequency value at which a peak in the alpha range (7–13 Hz) is observed, corrected for the aperiodic activity (1/f) of the power spectrum, ii) the alpha power value associated with that peak, also corrected for the 1/f, iii) the offset, corresponding to broadband shifts in the power spectrum; and iv) the exponent, which reflects the slope of the aperiodic component of the power spectrum.

Statistical differences in the topographies of periodic (IAF, alpha power) and aperiodic (offset, exponent) indexes recorded before and after tACS for different stimulation Conditions (IAF, IAF+2 Hz, IAF-2 Hz) were assessed using two-tailed non-parametric permutations tests with cluster-based correction for multiple comparisons (number of randomizations = 2500) (Maris and Oostenveld, 2007). Aperiodic parametrization and statistical analysis were conducted using the Fieldtrip toolbox (version 20.230.118) for MATLAB (Oostenveld et al., 2011).

3. Results

3.1. Modulation of temporal segregation processes

The Chi-square test performed on a generalized linear mixed-effects model of 2-flash accuracy data revealed a significant interaction between Condition and Hemifield, $\chi(2) = 7.329$, $p = 0.026$. In the direction of our hypothesis, post-hoc tests showed an increased 2-flash accuracy for the IAF+2 Hz Condition as opposed to the IAF-2 Hz Condition, specifically in the right hemifield (z-ratio = −2.770, $p_{FDR} = 0.008$, Fig. 2A). Interestingly, the same effect was not observed for 2-flash stimuli presented in the left hemifield (z-ratio = −0.203, $p_{FDR} = 0.839$). A significant interaction was also found between ISI and Hemifield, $\chi(1) = 40.947$, $p < 0.001$, showing that 2-flash accuracy was higher for stimuli presented on the right compared to the left hemifield across ISI levels (all $ps_{FDR} < 0.0001$, Fig. 2B). Furthermore, we found a main effect of IAF, $\chi(1) = 5.091$, $p = 0.024$, showing that 2-flash accuracy increased as a function of resting-state IAF (Fig. 2C) in line with previous correlational results (Deodato and Melcher, 2023; Samaha and Postle, 2015). Main effects of ISI, $\chi(1) = 5909.246$, $p < 0.001$, and Hemifield $\chi(1) = 478.507$, $p < 0.001$, were not further analyzed considering their involvement in more complex interaction effects described above. The control analysis performed on 1-flash accuracy revealed only a main effect of Hemifield ($\chi(1) = 154.394$, $p < 0.001$, suggesting that the aforementioned significant effects are specific to the accurate discrimination of 2 flashes (i.e., temporal segregation). Full results of the two models are reported in supplementary materials, tables S2-S5.

3.2. Modulation of alpha power and frequency

Next, we investigated if the online behavioral change of 2-flash accuracy as a function of the stimulation Condition was followed by short-term neurophysiological modulations in alpha frequency or power. To do so, non-parametric tests comparing resting-state IAF and alpha peak power before and after stimulation in the three Conditions (IAF, IAF+2 Hz, IAF-2 Hz) were performed with a cluster-based correction for multiple comparisons. No significant cluster emerged when comparing IAF before and after stimulation in either Condition (see Figure S1A in Supplementary Materials). When comparing resting-state alpha peak power, we found a significant cluster of occipito-parietal electrodes showing decreased alpha peak power following tACS (Fig. 3A, see also Figure S1B in Supplementary Materials). This effect was present across conditions (IAF, $p_{cluster} = 0.002$; IAF+2 Hz, $p_{cluster} = 0.008$; and IAF-2 Hz $p_{cluster} = 0.005$).

3.3. Modulation of aperiodic slope and offset

Finally, we also explored the aperiodic component of the power spectrum to investigate if tACS could modulate the E/I balance. Similarly to the oscillatory analysis, we performed cluster-based permutation tests to investigate resting-state changes before and after stimulation in the aperiodic exponent (i.e., the slope of the power spectrum) and the offset (i.e., the broadband power across frequencies). Fig. 3B shows a modulation of the aperiodic exponent in the IAF+2 Hz Condition ($p_{cluster} = 0.006$), suggesting that the exponent was reduced following tACS at higher frequencies (see also Figure S1C in Supplementary Materials). A shift in the aperiodic exponent can also lead to a variation of the offset, which was indeed present in the IAF+2 Hz Condition ($p_{cluster} = 0.002$), indicating that offset values reduced following stimulation at higher

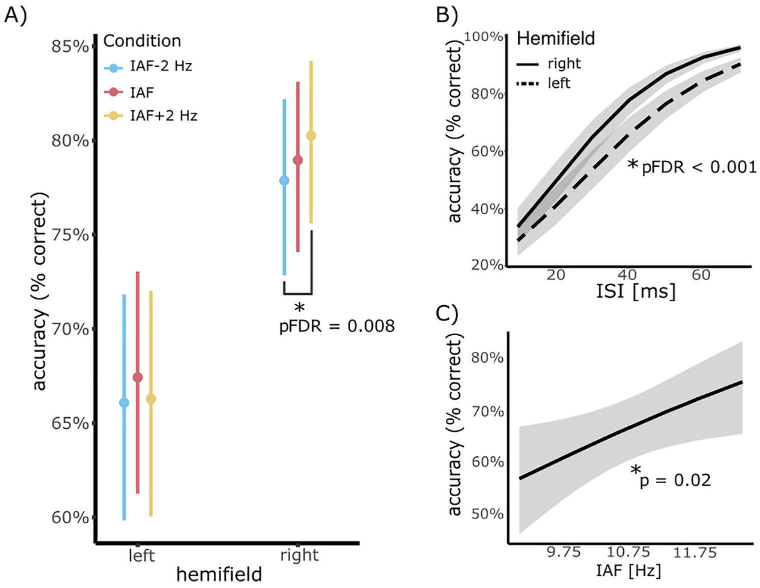

Fig. 2. Predicted values of 2-flash accuracy. A) A generalized linear mixed-effects model on accuracy data revealed an interaction between Condition and Hemifield, indicating that 2-flash accuracy increased as a function of stimulation frequency only for stimuli presented in the right hemifield. Error bars represent 95 % confidence intervals. B) An interhemispheric advantage for stimuli presented on the right was observed across ISI levels. The solid (for 2-flashes presented on the right hemifield) and dashed (for 2-flashes on the left hemifield) lines and the shaded areas represent the prediction and confidence intervals of the associated linear model. C) Resting-state IAF (before any stimulation) predicted 2-flash accuracy. The solid line and the shaded area represent the prediction and confidence intervals of the associated linear model. ISI = Interstimulus Interval; IAF = Individual Alpha Frequency.

frequencies over occipito-parietal electrodes (see Figure S1D and Figure S2 in the Supplementary Materials).

4. Discussion

The present study aimed to investigate the relationship between alpha-band oscillations and visual temporal sampling mechanisms through the application of bilateral HD-tACS. At the behavioral level, we found that stimulation delivered at off-peak alpha frequencies can shift temporal processing of rapidly presented visual events. As expected, tACS at IAF-2 Hz led to a decrease in temporal segregation accuracy in comparison to stimulation at IAF+2 Hz, which enhanced task performance. This effect was specific for stimuli presented in the right hemifield. Furthermore, we corroborated previous correlational evidence by showing that baseline resting-state IAF predicted 2-flash accuracy, with higher alpha frequencies being linked to better temporal segregation ability (Samaha and Romei, 2024). Regarding resting-state EEG modulations, we found no shift in IAF following tACS, but a reduction of alpha peak power across all stimulation conditions. We also found a modulation of aperiodic indices of the power spectrum following stimulation at IAF+2 Hz, indicating that both the aperiodic exponent (i.e., the 1/f slope of the power spectrum) and offset (i.e., broadband power across frequencies) were reduced after stimulation.

Taken together, these results support the hypothesis that posterior alpha oscillations play a crucial role in determining visual sampling processes, a link that has been recently questioned by null results (Buergers and Noppeney, 2022; London et al., 2022; but see also Samaha and Romei, 2024). Furthermore, these findings offer new evidence that tACS can influence alpha rhythms and temporal perception within the visual domain, contributing to the body of research showing the effects of tACS on illusory (Cecere et al., 2015; Minami and Amano, 2017) and time perception (Mioni et al., 2020). To our knowledge, only two previous studies employed tACS to investigate temporal segregation/integration processes within the visual modality. Battaglini and colleagues (2020) employed alpha (10 Hz), beta (18 Hz) and sham HD-tACS. The authors reported that alpha stimulation significantly lowered two flash rates in a 2FFT as compared to beta stimulation when adding the IAF as a covariate in the analysis. On the other hand, Ronconi et al. (2022) tested participants with a more complex segregation/integration task alongside with an individualized stimulation at off-peak frequencies but did not report significant effects. It is important to note that the difference in results across studies might relate to variations in montage design. Specifically, both Battaglini et al. (2020) and Ronconi et al. (2022) employed a right-lateralized stimulation montage, with the former targeting occipito-parietal electrodes (PO8) and the latter targeting parietal electrodes (P4). Here, we adopted a bilateral montage and targeted occipito-parietal electrodes (PO7 and PO8). Given the focality of HD-tACS, the choice of the stimulated region as well as stimulation intensity might be crucial for a behavioral modulation to occur (Ronconi et al., 2022). A further important choice in montage design is the decision between bilateral and unilateral stimulation, especially given the advantage in detecting stimuli in the right hemifield shown in our results. Inter-hemispheric differences in visuo-spatial ability are well documented, and the right hemisphere is typically regarded as dominant in attentional orientation across both hemispheres (Duecker and Sack, 2015; O'Regan and Serrien, 2018; Suchan et al., 2012). On the other hand, the left hemisphere may be more specialized in the temporal aspects of attentional allocation rather than spatial ones. This is supported by previous reports showing a stronger modulation of left parietal and extra-striatal visual areas in response to temporal rather than spatial allocation of attentional resources (Coull and Nobre, 1998; Macaluso and Frith, 2000). Inter-hemispheric differences are not only observed in behavior, but also in the characterization of alpha oscillations. For example, it has been shown that visual detection performance fluctuates at lower alpha frequencies for stimuli presented in the right hemifield (Gallina et al., 2024). The left hemisphere is also characterized by lower power of posterior alpha following the orientation of spatial attention (Gallotto et al., 2020). Thus, it is possible that the lateralization of the behavioral effects of the present study might relate to hemispheric asymmetries in alpha rhythms, making them more or less susceptible to tACS modulation. For example, it has been demonstrated that a lower baseline alpha power is required for entrainment to occur; in other words, a high alpha power at baseline could not be further enhanced by stimulation (Neuling et al., 2013; Trajkovic et al., 2024). In line with this

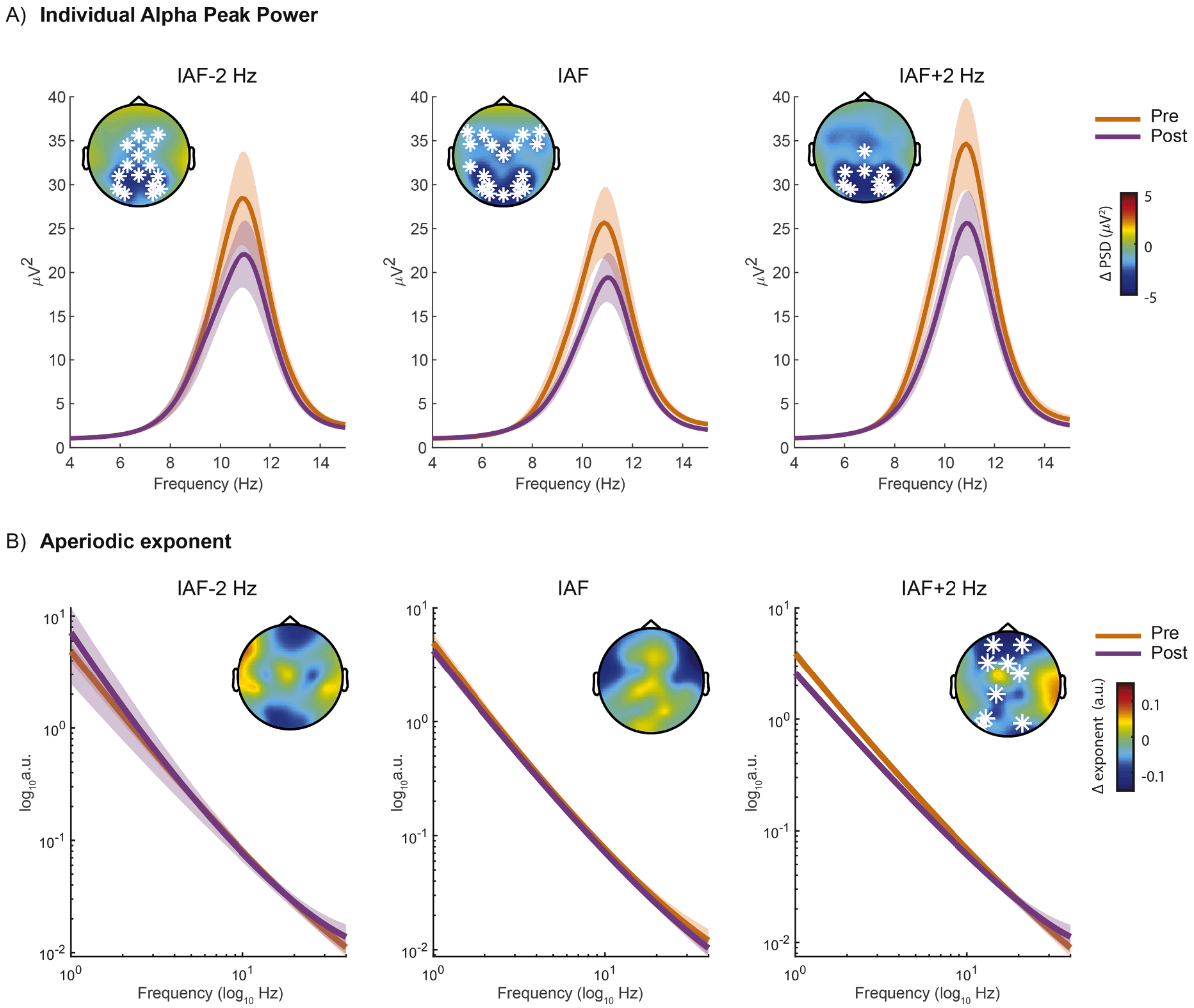

Fig. 3. Resting state EEG results. A) FFT power spectra averaged over significant electrodes in the cluster depicting power differences in the IAF across stimulation conditions (IAF-2 Hz, IAF, IAF+2 Hz) before ("Pre") and after ("Post") tACS. Topographies represent differences in alpha power corresponding to the IAF, computed by subtracting power in the "Post" session from the one recorded in the "Pre" session. B) Similarly, FFT power spectra averaged over significant electrodes in the cluster depict differences in the aperiodic exponent (i.e., the 1/f slope) of the power spectrum across stimulation conditions before ("Pre") and after ("Post") tACS. Topographies represent differences in the aperiodic exponent, computed by subtracting the exponent in the "Post" session from the one recorded in the "Pre" session. Channels that were included in the significant clusters in the permutation tests are marked with white asterisks in the topographies. Shaded coloured areas represent SEM. IAF = Individual Alpha Frequency.

idea, left but not right-lateralized tACS delivered at alpha frequencies over occipito-parietal areas modulated endogenous spatial attention in previous studies (Kasten et al. 2020; Radecke et al., 2023; Schuhmann et al., 2019).

Despite the behavioral modulation in the direction of the tACS frequency, we found no shift in IAF following stimulation. This result is aligned with previous evidence showing that tACS at off peak frequencies does not modulate resting-state IAF post-stimulation (for a meta-analysis, see Millard et al., 2024). Indeed, neurophysiological changes possibly related to entrainment, which would predict a shift of the endogenous IAF in the direction of the stimulation frequency, might be short-lived and not captured offline when the EEG is recorded (Vossen et al., 2015). Alternatively, the lack of condition-specific neurophysiological changes following stimulation might reflect insufficient stimulation intensity to induce sustained entrainment effects. While our stimulation protocol was informed by prior studies employing comparable HD-tACS montages and intensities (Battaglini et al., 2020; Di Dona et al., 2024; Kemmerer et al., 2022), recent non-human primate studies have shown that neural entrainment typically occurs at electric field strengths of approximately 0.3 mV/mm, which correspond to stimulation intensities of $\geq$2 mA in humans (Wischnewski et al., 2023). Thus, the present results caution against drawing firm conclusions about entrainment accounts of tACS or a causal role of alpha frequency per se in visual temporal sampling.

Previous literature has reported a sustained increase of alpha power following tACS (De Koninck et al., 2021; Kasten et al., 2016, 2024; Neuling et al., 2013; Wang et al., 2022). These changes in oscillatory power have been previously ascribed to plastic changes in oscillatory circuits as well as in cortical excitability following stimulation (such as STDP), longer lasting than entrainment effects (Vossen et al., 2015). Alpha power also increases naturally, as a consequence of time on task and mental fatigue (Benwell et al., 2019; Boksem et al., 2005). Thus, it is interesting to note that here we report a general decrease of alpha power following tACS at any stimulation frequency, within a broad cluster of occipito-parietal and central electrodes. To our knowledge, this effect has been rarely reported in previous literature. First, Helfrich et al. (2014) observed a reduction of alpha power following tACS at 40 Hz over extrastriate visual areas, a result that has been interpreted as a marker of gamma-band entrainment, given the antagonistic alpha-gamma interplay in parieto-occipital areas. Interestingly, a reduction of alpha and beta power was observed by Di Dona and colleagues (2024), who employed a similar bilateral HD montage to the one of the present study (stimulating P3 and P4 instead of PO7 and PO8), with the same intensity (0.8 mA peak-to-baseline) but with different frequency (18 Hz). However, this reduction of alpha power was present not only following active but also sham stimulation. In contrast, Battaglini et al. (2020) found no effect on power when stimulation was unilaterally delivered to the right MT/V5, whether at alpha, beta, or sham frequencies. Taken together, these results show a complex picture, where a decrease in power might reflect non-specific, task-related or contextual factors. Furthermore, alongside non-specific effects driven by contextual or task-related factors, a more precise characterization of different montages and their electrophysiological outcomes is necessary to understand the non-frequency-specific neurophysiological changes induced by tACS.

It is interesting to note that not only oscillatory, but also the aperiodic activity of the power spectrum is modulated in a frequency-specific way by tACS. Specifically, we observed a lower (flatter) aperiodic exponent following stimulation at higher alpha frequencies. Similarly, the observed change in the aperiodic offset might result from a change in the aperiodic exponent, with a lower offset resulting from a flatter power spectrum. Previous literature has suggested that the aperiodic activity of the power spectrum might reflect global changes in neural noise levels, with a flatter aperiodic spectrum indexing a preponderance towards cortical excitation in the E/I balance (Gao et al., 2017; Voytek and Knight, 2015). Furthermore, a flatter aperiodic exponent has been linked to increased background neuronal firing, which might in turn weaken local field power coherence and decrease neuronal synchronization (Buzsáki et al., 2012; Freeman and Zhai, 2009; Voytek and Knight, 2015). In line with this idea, we speculate that the observed increase in neural excitation following tACS at higher alpha frequencies (indexed by a flatter aperiodic exponent) might result from a desynchronization of the endogenous neural oscillations at the natural frequency (i.e., the IAF). In turns, behavioral performance might benefit by enhanced background neural excitation levels, in line with previous studies showing that increasing the level of stochastic noise in neuronal firing might lead to improved perceptual accuracy (Battaglini et al., 2023; Pavan et al., 2019). As discussed in Masina et al. (2025), characterizing aperiodic as well as periodic changes in the power spectrum following tACS provides a further insight to its long-lasting neurophysiological effects. Indeed, offline effects might not necessarily represent a proxy for online tACS-induced effects (Veniero et al., 2015). Periodic changes might reflect immediate/online effects in line with the entrainment/STDP hypotheses, while aperiodic activity might represent a possible marker of longer-lasting excitability changes following rhythmic stimulation, with cascade effects on neural synchronization and brain function. However, this interpretation remains speculatory, as to the present day pipelines that remove tACS artifacts from concurrent EEG recordings are exploratory and complex. Furthermore, the potential mechanisms driving differential E/I modulations in response to tACS at different stimulation frequencies have yet to be explored.

There are several limitations to the present studies that are worth discussing. First, it is important to acknowledge that the absence of a sham stimulation condition limits our ability to fully dissociate stimulation-induced effects from potential non-specific factors, such as fatigue or general time-on-task influences. This limitation is particularly relevant when interpreting the observed decrease in alpha power across all stimulation frequencies. While the within-subject design and the use of three distinct active stimulation frequencies allowed us to detect frequency-specific behavioral effects, the global reduction in alpha power could reflect unspecific effects that a sham condition would have helped to control for. Additionally, some stimulation parameters might have been suboptimal to assess the neurophysiological modulations following tACS. As discussed above, while our choice of stimulation intensity was in line with previous research and with safety guidelines, a stronger stimulation intensity might be necessary to induce entrainment-driven changes that might translate to sustained effects recorded offline. The systematic variation of stimulation parameters, outside of the scope of the present study, should be considered in future research to better delineate the conditions under which tACS can produce lasting neurophysiological modulations of the targeted frequency. Finally, neurophysiological results that were either unexpected, such as a reduction of alpha power across stimulation frequency, or linked to exploratory analyses, such as a frequency-specific modulation of aperiodic activity, should be interpreted with caution. These results, nonetheless, open new venues for investigation. For example, future research should investigate whether they represent context-dependent phenomena emerging from specific stimulation parameters as well as specific task demands and baseline neural states.

Additionally, while our findings provide novel insights into the effects of individualized alpha-frequency tACS on visual temporal perception, the extent to which these effects generalize to other forms of temporal processing or sensory modalities remains an important question for future research. In this regard, Mioni et al. (2020) demonstrated that a similar individualized tACS protocol modulated perceived duration in a time generalization task employing visual stimuli, with faster alpha stimulation leading to longer perceived intervals. In the audio-visual domain, Cecere et al. (2015) provided evidence of cross-modal effects of alpha-frequency stimulation on temporal perception, with faster alpha oscillations shrinking the temporal window the sound-induced double-flash illusion. These previous results support the idea that some degrees of generalizability to the broader temporal perception domain can be obtained with analogous neuromodulatory approaches.

5. Conclusions

The present study aimed at investigating the possibility of manipulating visual temporal segregation by means of tACS delivered at individualized alpha frequencies, in line with the hypothesis that alpha oscillations provide a timeframe for temporal sampling in the visual domain (Kristofferson, 1967b; Samaha and Postle, 2015). In line with this idea, we found that tACS delivered at faster alpha frequencies (compared to the IAF) resulted in improved temporal parsing. Vice versa, stimulation at lower alpha frequency deteriorated the accuracy in the processing of rapidly presented visual stimuli. Interestingly, this effect was specific for the right hemifield, in line with interhemispheric asymmetries in attentional processing and endogenous alpha rhythms. This behavioral effect was reflected by EEG modulations in the oscillatory and aperiodic components of the power spectrum, adding evidence to the body of literature investigating neurophysiological effects of non-invasive brain stimulation.

Data availability

The data that support the findings of this study are available from the authors, upon reasonable request.

CRediT authorship contribution statement

Alessia Santoni: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Giuseppe Di Dona:** Writing – review & editing, Software, Methodology, Investigation, Formal analysis. **Riccardo Gironi:** Investigation, Data curation. **Sara Stottmeier:** Investigation, Formal analysis. **Luca Battaglini:** Writing – review & editing, Project administration, Conceptualization. **Luca Ronconi:** Writing – review & editing, Writing – original draft, Supervision, Software, Resources, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2025.121474.

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