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μ-Transcranial Alternating Current Stimulation Induces Phasic Entrainment and Plastic Facilitation of Corticospinal Excitability

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ABSTRACT

Transcranial alternating current stimulation (tACS) has been proposed to modulate neural activity through two primary mechanisms: entrainment and neuroplasticity. The current study aimed to probe both of these mechanisms in the context of the sensorimotor μ-rhythm using transcranial magnetic stimulation (TMS) and electroencephalography (EEG) to assess entrainment of corticospinal excitability (CSE) during stimulation (i.e., online) and immediately following stimulation, as well as neuroplastic aftereffects on CSE and μ EEG power. Thirteen participants received three sessions of stimulation. Each session consisted of 90 trials of μ-tACS tailored to each participant's individual μ frequency (IMF), with each trial consisting of 16 s of tACS followed by 8 s of rest (for a total of 24 min of tACS and 12 min of rest per session). Motor-evoked potentials (MEPs) were acquired at the start and end of the session ($n = 41$), and additional MEPs were acquired across the different phases of tACS at three epochs within each tACS trial ($n = 90$ for each epoch): early online, late online and offline echo. Resting EEG activity was recorded at the start, end and throughout the tACS session. The data were then pooled across the three sessions for each participant to maximise the MEP sample size per participant. We present preliminary evidence of CSE entrainment persisting immediately beyond tACS and have also replicated the plastic CSE facilitation observed in previous μ-tACS studies, thus supporting both entrainment and neuroplasticity as mechanisms by which tACS can modulate neural activity.

1 | Introduction

Over the last two decades, researchers have used a type of non-invasive brain stimulation called transcranial alternating current stimulation (tACS) to experimentally modulate various aspects of cognition (e.g., attention, memory, perception and motor processes) by matching the frequency of the applied alternating current with the frequency of a given neural oscillation known to be associated with a particular cognitive task (for reviews, see Antal and Paulus 2013; Bland and Sale 2019; Herrmann et al. 2016; Vosskuhl, Strüber, and Herrmann 2018; Wischnewski, Alekseichuk, and Opitz 2023). However, despite promising cognitive effects, a thorough understanding of the underlying neurophysiological mechanisms is still required if this technique is to be used across a wide range of clinical settings, such as in psychiatry (Alexander et al. 2019; Elyamany et al. 2021) and neurorehabilitation (Del Felice et al. 2019; Yang, Yi, and Chang 2024).

At the neuronal level, tACS is considered a subthreshold stimulation in that it probabilistically influences the spike timing of pyramidal cells in a frequency- and phase-specific manner (Reato et al. 2010; Johnson et al. 2020; Tran, Shirinpour, and Opitz 2022; Vöröslakos et al. 2018), as opposed to directly causing the targeted cells to fire (Elyamany et al. 2021; Vosskuhl, Strüber, and Herrmann 2018). At the network level, however, there is growing evidence to suggest that these subtle changes in spike timing can lead to entrainment of endogenous oscillatory networks with respect to the frequency and phase of the applied stimulation (Ali, Sellers, and Frohlich 2013; Helfrich et al. 2014a, 2014b; Huang et al. 2021; Johnson et al. 2020; Krause et al. 2019, 2022; Reato et al. 2013, 2010; Tran, Shirinpour, and Opitz 2022; Wischnewski et al. 2024; Witkowski et al. 2016). This online entrainment is characterised by a resonance phenomenon known as an 'Arnold Tongue', where oscillations that deviate from the eigenfrequency (i.e., resonant frequency) of the network require greater current intensities in order to entrain to tACS (Ali, Sellers, and Frohlich 2013; Huang et al. 2021; Liu et al. 2018; Schutter and Wischnewski 2016; Thut et al. 2017; Vosskuhl, Strüber, and Herrmann 2018).

Although online entrainment has been proposed to persist briefly beyond stimulation (i.e., entrainment echoes; Hanslmayr, Matuschek, and Fellner 2014; Marshall et al. 2006; Thut et al. 2011; van Bree et al. 2021), longer lasting tACS aftereffects (i.e., up to 70 mins poststimulation; Kasten, Dowsett, and Herrmann 2016; Neuling, Rach, and Herrmann 2013) are more likely to be caused by changes in synaptic plasticity (Wischnewski et al. 2019). This does not, however, mean that entrainment and plastic aftereffects are mutually exclusive. In fact, it has been proposed that plastic aftereffects may still be mediated by online resonance dynamics and, thus, may be facilitated by (or dependent on) online entrainment (Helfrich et al. 2014a, 2014b; Veniero et al. 2015; Vossen, Gross, and Thut 2015; Zaehle, Rach, and Herrmann 2010).

Human studies investigating the mechanisms of tACS have traditionally used electroencephalography (EEG; Helfrich et al. 2014a, 2014b) or magnetoencephalography (MEG; Witkowski et al. 2016) to quantify the effects of tACS on endogenous neural activity. However, the presence of complex, non-linear tACS artefacts in the EEG/MEG signal makes definitively demonstrating entrainment in the EEG/MEG concurrently with tACS a difficult task (Kasten and Herrmann 2019; Noury, Hipp, and Siegel 2016; Noury and Siegel 2017). Although many analysis methods have been developed in an attempt to filter the tACS artefact from the EEG/MEG, none of these approaches have been successful in eliminating the artefact in its entirety (for review, see Kasten and Herrmann 2019; but see Bland 2021). Therefore, it is theoretically possible that previously reported entrainment effects in the EEG/MEG (Helfrich et al. 2014a; Witkowski et al. 2016) may reflect these residual artefacts rather than genuine entrainment of endogenous oscillations.

We have recently utilised a phase-dependent transcranial magnetic stimulation (TMS) protocol (Fehér, Nakataki, and Morishima 2017, 2022; Nakazono et al. 2021; Raco et al. 2016; Schaworonkow et al. 2018, 2019; Schilberg et al. 2018; Zrenner et al. 2018, 2022) as an alternative method for assessing entrainment to slow-wave tACS (Geffen, Bland, and Sale 2021). Here, TMS pulses are applied at random phases of tACS such that the TMS-induced motor-evoked potential (MEP) amplitudes (assessed via electromyography; EMG) provide an indirect assessment of corticospinal excitability (CSE; Bergmann et al. 2012; Di Lazzaro et al. 2004; Hallett 2007; Ilmoniemi and Kicić 2010) across the tACS phase cycle. Phase-dependent TMS can therefore be used to assess whether CSE, and in turn, endogenous neural activity, is entrained with respect to tACS phase. Crucially, unlike EEG, TMS–EMG measures are free of tACS artefacts, thus providing an unambiguous assessment of tACS-induced entrainment.

Although we did not observe entrainment of slow (0.75 Hz) oscillations in our previous phase-dependent TMS experiment (Geffen, Bland, and Sale 2021), this null result was primarily attributed to a lack of resonance dynamics between the eigenfrequency and tACS frequency (Ali, Sellers, and Frohlich 2013) as well as the relatively small MEP sample size per participant compared with simulation studies (Zoefel et al. 2019). The current study aimed to address both these limitations by using a tailored stimulation frequency that matches the eigenfrequency of the participants' sensorimotor cortex (i.e., the stimulation site) during wake, and by including multiple experiment sessions for each participant to maximise power (see Geffen, Bland, and Sale 2024).

Regarding the stimulation frequency, we chose to apply tACS in the alpha range (8–13 Hz). This was for two reasons. First, alpha oscillations are one of the most prominent oscillations in the sensorimotor cortex during wakeful rest, where they are referred to as the sensorimotor Mu (μ) rhythm (Craddock et al. 2017; Hari 2006; Weisz et al. 2014; Zhang and Ding 2010), and second, CSE has been shown to be modulated by endogenous μ phase, with greater MEP amplitudes at troughs compared with peaks (Baur et al. 2020; Berger et al. 2014; Bergmann et al. 2019; Hussain et al. 2018; Schaworonkow et al. 2018, 2019; Stefanou et al. 2018; Wischnewski et al. 2022; Zrenner et al. 2018, 2022, 2023). Contrary to alpha oscillations in the occipital cortex that are traditionally associated with inhibition of task-irrelevant areas (Herring et al. 2019; Jensen and Mazaheri 2010; Klimesch, Sauseng, and Hanslmayr 2007; Mathewson et al. 2011; Romei et al. 2008a, 2008b; Schalk 2015; Thut et al. 2006; van Dijk et al. 2008), sensorimotor μ oscillations have been suggested to reflect facilitation of CSE, either via active facilitation of task-relevant areas or via active inhibition of inhibitory interneurons to disinhibit task-relevant areas (Bergmann et al. 2019; Karabanov et al. 2021; Ogata et al. 2019; Schilberg et al. 2021; Thies et al. 2018). Although recent μ-tACS studies have reported facilitatory plastic aftereffects on CSE (Feurra et al. 2019; Fresnoza et al. 2018; Madsen et al. 2019; Schilberg et al. 2018), only two of these studies (Madsen et al. 2019; Schilberg et al. 2018) assessed the relationship between μ-tACS phase and CSE, neither of which found any significant phasic modulation of MEP amplitudes. Therefore, there remains a crucial need for further investigation of both the acute phasic effects and sustained aftereffects of μ-tACS on CSE. Therefore, the aims of this experiment were to firstly investigate phasic entrainment of CSE to the phase of intermittent μ-tACS, both during (i.e., online entrainment) and immediately following (i.e., entrainment

echoes) stimulation; second, to investigate the sustained aftereffects of μ-tACS on CSE and μ EEG power. It was hypothesised that μ-tACS would induce μ-rhythm-like sinusoidal changes in CSE that correspond with the tACS phase, demonstrating online entrainment. Second, sinusoidal changes in CSE would persist for the first oscillatory cycle immediately following each trial of stimulation, thus demonstrating entrainment echoes. Third, CSE and μ EEG power would increase across the total stimulation period, and these increases would then be sustained beyond the stimulation period, consistent with plastic aftereffects.

2 | Materials and Methods

2.1 | Subjects

Thirteen neurotypical, right-handed participants were recruited for the experiment (5 male, mean age = 23 ± 4 years). Crucially, we opted to have each participant complete three separate experiment sessions (with a minimum of 1 week between sessions) to ensure that the MEP sample size per participant would be sufficient for assessing phasic entrainment of MEP amplitudes (see Zoefel et al. 2019). We recently demonstrated in a simulated environment that this approach can improve the statistical power of phasic analyses compared with the traditional approach of performing just one session per participant on a greater number of participants (Geffen, Bland, and Sale 2024). All participants completed a safety screening questionnaire (Keel, Smith, and Wassermann 2001; Rossi et al. 2021) and provided a written statement of informed consent prior to commencing the experiment. The exclusion criteria from this safety screen included personal or family history of epilepsy/seizures, medication that could affect seizure threshold, history of brain injury/condition (e.g., stroke and concussion), implanted devices or metal in the head, frequent or severe headaches or current pregnancy. Throughout each session, participants were instructed to relax, avoid moving their hands and avoid doing any mentally stimulating tasks in their head (e.g., simple math) but also to keep their eyes open and stay awake. Approval was granted by The University of Queensland Human Research Ethics Committee.

2.2 | Experimental Setup

2.2.1 | tACS/TMS

The target site for stimulation was the hand area of the left primary motor cortex ($M1_{HAND}$; typically corresponds with the EEG coordinate C3), specifically the region associated with the right *first dorsal interosseous* (FDI; primary target muscle) and *abductor digiti minimi* (ADM; secondary target muscle) muscles of the second and fifth digits, respectively.

TMS pulses were applied via a Magstim Double 70-mm Remote Control Coil charged by a Magstim 200^2 stimulator (Magstim, UK). Manual TMS 'hot-spotting' (Rossini et al. 1994) was performed to determine each participant's individual location for the left $M1_{HAND}$ region as well as the TMS intensity required to consistently induce MEPs in the FDI (i.e., our primary target muscle) with amplitudes of ~1 mV (Cuypers, Thijs, and Meesen 2014; Ogata et al. 2019; Thies et al. 2018). Here, the position of the TMS coil and the stimulation intensity were systematically adjusted until MEPs were consistently induced with amplitudes around the target amplitude. For some participants (3 total, not included in the reported sample size), MEPs of this amplitude could not be consistently induced during hot-spotting at intensities < 80% of the maximum stimulator output, and so these participants did not take any further part in the study. This threshold was set to avoid overheating of the TMS coil mid-session at intensities above 80% of maximum stimulator output. The location of the left $M1_{HAND}$ region was marked on the participant's scalp using an erasable marker.

tACS was applied via a NeuroConn DC Stimulator Plus using a classical M1-contralateral supraorbital region electrode montage (Heise et al. 2016), with the target electrode placed ~2 cm posterolateral to the marked hotspot (around Cp3) and the return electrode placed over the contralateral supraorbital region. This slight posterolateral shift for the M1 electrode is thought to enhance the effectiveness of tACS by reducing current shunting through the scalp and cerebrospinal fluid to maximise the current density at M1 (Faria, Hallett, and Miranda 2011; Laakso et al. 2016). The scalp was first rubbed with ethanol (70%), then Ten20 conductive paste (Weaver and Company) was applied to both 42 × 45 mm pad electrodes before placing them onto their respective positions on the scalp. The cable for the M1 electrode was oriented inferiorly, whereas the cable for the supraorbital region electrode was oriented laterally.

2.2.2 | EMG/EEG

EMG activity for the FDI and ADM muscles was recorded via disposable surface electrodes (H124SG 30 mm × 24 mm). For both muscles, one electrode was placed on the relevant muscle belly and the other on the nearby metacarpophalangeal joint, with reference electrodes placed over the palmar aspect of the distal forearm.

EEG activity was recorded using 66 reusable surface electrodes (64 active electrodes in 10:20 layout + 2 reference electrodes) embedded in a cap (Biosemi CAP S/M/L 64 10/20). The EEG electrodes directly above the tACS pad electrodes had to be removed as the resultant artefacts exceeded the acceptable limit of the EEG system, preventing EEG data acquisition. The specific EEG channels that needed to be removed varied slightly between participants because of individual differences in tACS electrode placement. For the tACS pad targeting $M1_{HAND}$, EEG channels C1 and C3 were removed for all sessions, channels Cp1 and Cp3 were removed for all but one participant, and channels Fc1 and Fc3 were removed for four participants. For the tACS pad over the contralateral supraorbital region, removed channels included Fpz, Fp2, Af4 and Af8.

Additional TMS hot-spotting was performed following the addition of the EEG cap, as the cap obscures the original marked hotspot whilst also slightly increasing the distance between the scalp and the TMS coil, and in most cases, the TMS intensity required to consistently induce MEPs around the target amplitude (Farzan et al. 2016; Ilmoniemi and Kicić 2010). This increased distance between the scalp and coil was minimised by removing the plastic wells for the EEG electrodes directly above the

M1 tACS pad electrode. The revised hotspot was marked on the EEG cap using tape and an erasable marker.

2.3 | Data Collection

EEG electrode measurements were captured (2048 Hz sampling rate) using a Biosemi ActiveTwo AD-Box (Biosemi, Amsterdam, Netherlands). EMG electrode measurements for both the FDI and ADM were acquired (1 kHz sampling rate, 20–1000 Hz band pass filtering) via an electrode adaptor (Model CED1902), before being amplified by a CED1902, and finally recorded by a CED1401 MICRO3 (Cambridge Electronic Designs, Cambridge, UK). TMS triggers were directly recorded by the CED1401 MICRO3 and were also recorded by the ActiveTwo EEG system via an MMBT-S Trigger Interface Box. The EMG data were then transferred from the CED1401 MICRO3 to a PC and saved via Signal software (6.04; Cambridge Electronic Designs, Cambridge, UK), whereas the EEG data were transferred from the ActiveTwo AD-Box to a separate PC and saved via ActiView (Ver. 8.08) software (Biosemi, Amsterdam, Netherlands). Both EMG and EEG data were then exported to MATLAB (Ver. R2020b) and subsequently JASP (Ver. 0.14.1.0) for analysis.

2.4 | Experimental Procedure

2.4.1 | EEG Paradigm

Before commencing the experiment, EEG activity was recorded for 5 min of wakeful (eyes open) rest and analysed using a Welch's power spectral density estimate (see Section 2.5.1) to determine each participant's individual μ frequency (IMF), which was used as the stimulation frequency for tACS. The IMF was defined objectively as the frequency with the greatest spectral power from 8 to 13 Hz (at a resolution of 0.5 Hz), even if the frequency spectrum included multiple peak frequencies with similar power values (e.g., from a broad peak around a particular frequency or from multiple peaks across different frequencies). EEG was also recorded throughout the tACS delivery to provide a measure of the tACS output, which allowed us to determine when TMS pulses were applied relative to the tACS phase, as well as to provide resting EEG data for the two 5-min break periods (see tACS Paradigm section below). Finally, an additional 5 min of resting EEG data was recorded at the end of the experiment session (i.e., post-tACS).

2.4.2 | tACS Paradigm

To desensitise the participants to the tACS sensations, each participant received an initial 'test' tACS paradigm after the electrodes were attached, consisting of 30 s of tACS at an intensity of 2 mA and a generic frequency of 10 Hz with an additional 5 s of ramp up/down at the start and end of the stimulation paradigm. For the actual tACS paradigm (Figure 1), participants received 90 trials of tACS in each experiment session, with each trial consisting of 16 s of tACS ('online') at an intensity of 2 mA peak-to-peak (see Alekseichuk, Wischnewski, and Opitz 2022) and a frequency that was tailored to the participant's IMF, followed by 8 s of no tACS ('offline'), for a total of 24 min of tACS and 12 min of no tACS (Figure 1A). The entire stimulation period was divided into three blocks (12 min comprising 30 trials each), with 5-min break periods (no stimulation delivered) between blocks. This allowed us to record continuous periods of EEG activity within the stimulation session without the presence of tACS artefacts, whilst also allowing the TMS coil to cool.

2.4.3 | TMS Paradigm

TMS pulses were applied at three epochs within each trial (1 MEP per epoch per trial, 90 MEPs per epoch per session, 270 MEPs per epoch across the three sessions): early online (~0.1–0.2 s after tACS had started), late online (~8.1–8.2 s after tACS had started) and offline echo (~0.1–0.2 s after tACS had ended).

To examine the phasic effects of μ-tACS on CSE (both online and offline), sufficient MEPs needed to be acquired across the different phases of the tACS waveform. This was achieved by implementing a 'jitter' (i.e., a randomised time delay that covers the length of a single tACS cycle; see Figure 1B) to the delivery of TMS so that it was not locked to a specific phase of tACS, and thus, TMS pulses were approximately uniformly delivered across the phase of the tACS cycle.

To examine the aftereffects of the entire tACS paradigm on CSE, 41 MEPs were also acquired at baseline and at the end of the entire period of tACS delivery (delivered at ~0.2 Hz).

2.5 | Statistical Analysis

2.5.1 | Data Processing/Transformation

The EEG data were imported to MATLAB (Ver. 2020b) via the EEGLAB toolbox (Delorme and Makeig 2004). The pre-/post-tACS data were imported directly, whereas the data from the two break periods had to first be extracted from the continuous EEG file for the tACS period. The data from each 5-min rest period (pre-tACS, Break 1, Break 2 and post) was then detrended, band-pass filtered (1–40 Hz) and cleaned using the 'clean_rawdata' EEGLAB function, which automatically identifies and excludes artefacts (e.g., eye blinks) and bad channels (i.e., channels with a flat or noisy signal). Spectral powers for channels Fc1, Fc3, Fc5, C1, C3, C5, Cp1, Cp3 and Cp5 were calculated using a Welch's power spectral density estimate, and then the powers were averaged across channels. The mean power values were then log transformed and the lowest value was subtracted from all other values (to ensure all values were positive). Finally, the absolute powers for μ (8–13 Hz) and IMF (±1 Hz) were converted to relative powers by dividing each of the absolute powers by the sum of powers for all frequencies.

It should be noted that because of the placement of the tACS pad over M1, any EEG electrodes that would be in contact with the tACS pad had to be physically removed to prevent the EEG from clipping, and unfortunately, this included some of the target electrodes for our spectral analysis. Furthermore, the exact electrodes that had to be removed would vary between participants depending on their individualised M1 location. C1 and C3 were

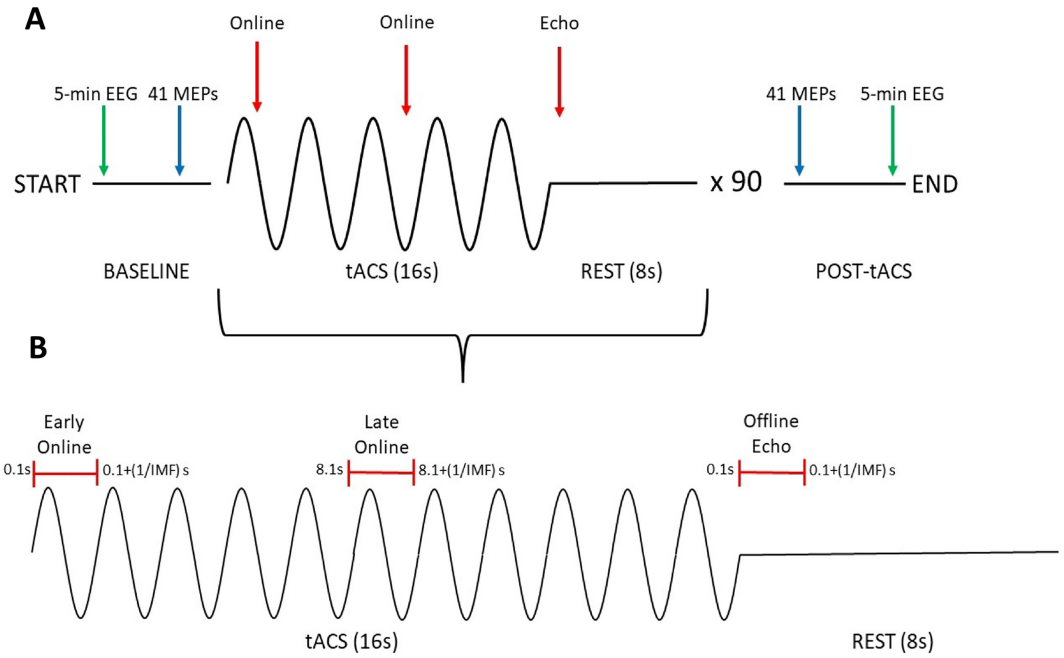

FIGURE 1 | Experimental procedure for probing changes in CSE induced by μ-tACS. (A) The experimental session consisted of a 16-s tACS period (represented as sine waves) followed by an 8-s rest period (represented as flat lines), repeated 90 times for a total of 36 min. Resting EEG activity was recorded for 5 min (green arrows) at the start of the session to determine each participant's IMF, as well as at two 5-min breaks (at 12 and 24 min, not shown in the figure) and at the end of the session to assess any tACS-induced changes in oscillatory activity. To assess the aftereffects of μ-tACS on CSE, 41 TMS-induced MEPs were acquired at the start and the end of the experimental session (blue arrows). To assess the phasic effects of μ-tACS on CSE online to and immediately following tACS, 2 MEPs were acquired within each tACS period and 1 MEP was acquired within each rest period (red arrows). (B) To probe the phasic effects of μ-tACS on CSE (both online and offline), MEPs were acquired at three epochs within each tACS trial (1 MEP per epoch per trial, 90 MEPs per epoch per session, 270 MEPs per epoch across the three sessions): early online, late online and offline echo. TMS pulses were applied with a 'jitter' (i.e., randomised time delay equal) that covers the length of a single tACS cycle (i.e., 1/IMF) so that pulses are approximately uniformly delivered across the different phases of tACS.

removed for all sessions and typically either Fc1 + 3 or Cp1 + Cp3 were removed depending on whether the participant's M1 was located more anteriorly or posteriorly, respectively. Therefore, any removed electrodes were interpolated using the data from their surrounding electrodes.

Unfortunately, after the data collection for the experiment had been completed, it was discovered that the 'clean_rawdata' function had not been performing the channel interpolation as expected and instead had removed the unclean channels entirely (both the physically removed channels as well as any other channels that 'clean_rawdata' had identified as unclean). This caused the remaining clean channels to be assigned to different channel numbers, resulting in an indexing error where some of the channels that were selected for spectral analysis had been replaced by other channels (i.e., not from the list of targeted channels) for some of the sessions. It should also be noted that for the initial IMF estimates, the EEG data were re-referenced to the common average; however, subsequent analyses were performed on data using the 'native' EEG reference electrodes ('CMS' and 'DRL'), since it was found that the common average re-referencing was unnecessary and, in some cases, resulted in subtle artefacts that interfered with the spectral analyses.

After fixing the channel interpolation using the 'pop_interp' EEGLAB function and reperforming the spectral analyses using the correct channels and the native reference electrodes, it was found that the revised pre-tACS IMF estimate (i.e., the endogenous eigenfrequency) differed from the initial pre-tACS IMF estimate (i.e., the stimulation frequency) for 15 out of the 39 sessions (eight from the indexing error and seven from the change in referencing), with the differences between the initial and revised estimates ranging from 0.5 to 3 Hz. These changes to the indexing and referencing were subsequently applied for the remaining EEG analyses. It should be noted that the spectral power analyses for IMF ± 1 Hz were performed with respect to the initial IMF estimates rather than the revised IMF estimates, since tACS-induced entrainment is expected to occur specifically with respect to the stimulation frequency rather than the endogenous eigenfrequency (Ali, Sellers, and Frohlich 2013; Krause et al. 2022). Although we initially considered discarding the incorrectly targeted sessions, we felt that the inclusion of these data could provide valuable information regarding the necessity to accurately target the IMF. Therefore, we have included all sessions in the analysis (described below).

The MEP exclusion criteria were identical to those used in our previous experiment (Geffen, Bland, and Sale 2021) and included the first MEP for each data set (as well as the first MEP after each of the break periods), which may be larger (Brasil-Neto, Cohen, and Hallett 1994) and more variable (Schmidt et al. 2009) than subsequent MEPs, as well as any MEPs with voluntary EMG activity detected in the 500 ms prior to TMS delivery (~1%–2% of MEPs excluded).

The TMS triggers were automatically categorised into their respective epochs (i.e., early online, late online and offline echo), and the tACS phase for the posterior electrode (i.e., over M1) was calculated using the EEG data from channel Oz. Phase was calculated around the 'late online' triggers, since these triggers are the only ones where tACS was present both before and after TMS was applied, thus providing the most reliable estimate of tACS phase. The computed phase for the late online triggers was then extrapolated (both forward and backward), and its values were computed at each of the other epochs, since we expect the tACS phase to continue into the offline period if entrainment persists beyond stimulation.

2.6 | Data Analysis

To assess the phasic entrainment of MEPs with respect to tACS phase, a permutation analysis was performed. Here, an ideal (best-fitting) sinusoidal model was fitted to each participant's observed MEPs (~270 MEPs pooled across three sessions for each epoch) based on their tACS phase (Bland and Sale 2019). The MEPs were then shuffled with respect to their phases for a total of 1000 permutations per participant and new sinusoidal models were fitted to the shuffled data. The amplitudes of these true and shuffled sinusoidal models were then compared, with the individual *p*-values representing the proportion of sinusoidal models fitted to the shuffled permutations of the true data that had an amplitude greater than that of the model fitted to the true data, remembering that under the null hypothesis (which assumes that the MEP amplitudes are not phase-dependent), the amplitudes of the sinusoidal models should be small (i.e., closer to zero). Because the permutation procedure disrupts any phasic effects that may be present, the shuffled MEPs act as a negative control for the true MEPs, and thus, the permutation analysis does not require a sham stimulation condition as a negative control. The group *p*-value for each muscle/timepoint was then obtained by combining the individual *p*-values using Fisher's method (Fisher 1992) as outlined in Zoefel et al. (2019).

To determine if there was a significant difference in mean MEP amplitudes between the pre- and post-tACS MEPs (40 each per session, 120 across the three sessions), two-way repeated measures ANOVAs (rmANOVA) were performed with *STIMULATION* (pre, post) and *SESSION* (1, 2, 3) as the two repeated measures factors (to confirm that there were no significant differences between the three sessions). To determine if there was a significant difference in mean MEP amplitudes between the online MEPs (540 across the three sessions) and the offline echo MEPs (270 across the three sessions) or between the three tACS blocks (180 online MEPs and 90 offline echo MEPs per block across the three sessions), a three-way repeated measures ANOVA was performed with *STIMULATION* (online, offline), *BLOCK* (1, 2, 3) and *SESSION* (1, 2, 3) as the three repeated measures factors. Post hoc *t*-tests (corrected for multiple comparisons using Holm's method) were then performed to compare the individual groups against each other. To examine how offline changes in MEP amplitudes evolved throughout the tACS period, mean MEP amplitudes for the pre- and post-tACS MEPs (120 each across the three sessions) and the offline MEPs of each tACS block (90 per block across the three sessions) were compared using a two-way repeated measures ANOVA with *TIME* (five levels: pre-tACS, post-tACS and the offline MEPs for the three tACS blocks) and *SESSION* (1, 2, 3) as the two repeated measures factors. Again, post hoc *t*-tests were then performed to compare the individual factors against each other.

To examine the effects of the tACS paradigm on both μ (8–13 Hz) and IMF (±1 Hz) relative spectral power, a two-way repeated measures ANOVA was performed with *TIME* (four levels: pre-tACS, post-tACS and the two break periods) and *SESSION* (1, 2, 3) as the two repeated measures factors. Again, post hoc *t*-tests were then performed to compare the individual factors against each other. For the repeated measures ANOVAs, standardised effect sizes for any significant differences were calculated as η^2 values. For the post hoc *t*-tests, standardised effect sizes for any significant differences were calculated as Cohen's *d* values.

We later performed separate analyses for the sessions that showed a difference between initial and revised IMF estimates (henceforth referred to as 'affected' sessions) and the sessions that did not show a difference (henceforth referred to as 'unaffected' sessions). However, because the number of affected and unaffected sessions varied between participants, most of these separate analyses had to be performed using data that had been averaged across the affected/unaffected sessions for each participant rather than including SESSION as a repeated measures factor (except for the permutation analysis where the data was simply pooled across the affected/unaffected sessions rather than being pooled across all sessions). Furthermore, we have also performed a correlational analysis comparing the absolute error in frequency targeting against the magnitude of entrainment/plasticity for each individual session.

3 | Results

3.1 | Phase-Specific Effects of μ-tACS on MEP Amplitude

The acute phase-specific effects of μ-tACS on MEP amplitudes were assessed by a permutation analysis. Ideal sinusoidal models were fitted to each participant's observed MEP amplitudes based on their tACS phase for each epoch (~90 MEPs per epoch per session, ~270 MEPs per epoch per participant; see Figure 2), and the amplitudes of these sinusoidal models were compared with the amplitudes of sinusoidal models fitted to 1000 permutations of the MEPs. The individual and group *p*-values for each muscle and epoch are listed in Table 1 and summarised in Figure S1. Fitted sinusoidal models with $p < 0.05$ are shown in Figure 2.

3.1.1 | Target Muscle (FDI) MEP Amplitudes

As shown in Table 1A, Participants 6, 7 and 12 showed significant phasic entrainment of FDI MEP amplitudes for the early online MEPs. Participant 3 showed significant entrainment for the late online MEPs. Finally, Participants 1, 5 and 9 showed significant entrainment for the offline echo MEPs. The group analysis revealed significant entrainment for the offline echo MEPs ($p = 0.021$) but no entrainment for either of the online MEPs, although the early online MEPs approached significance ($p = 0.081$).

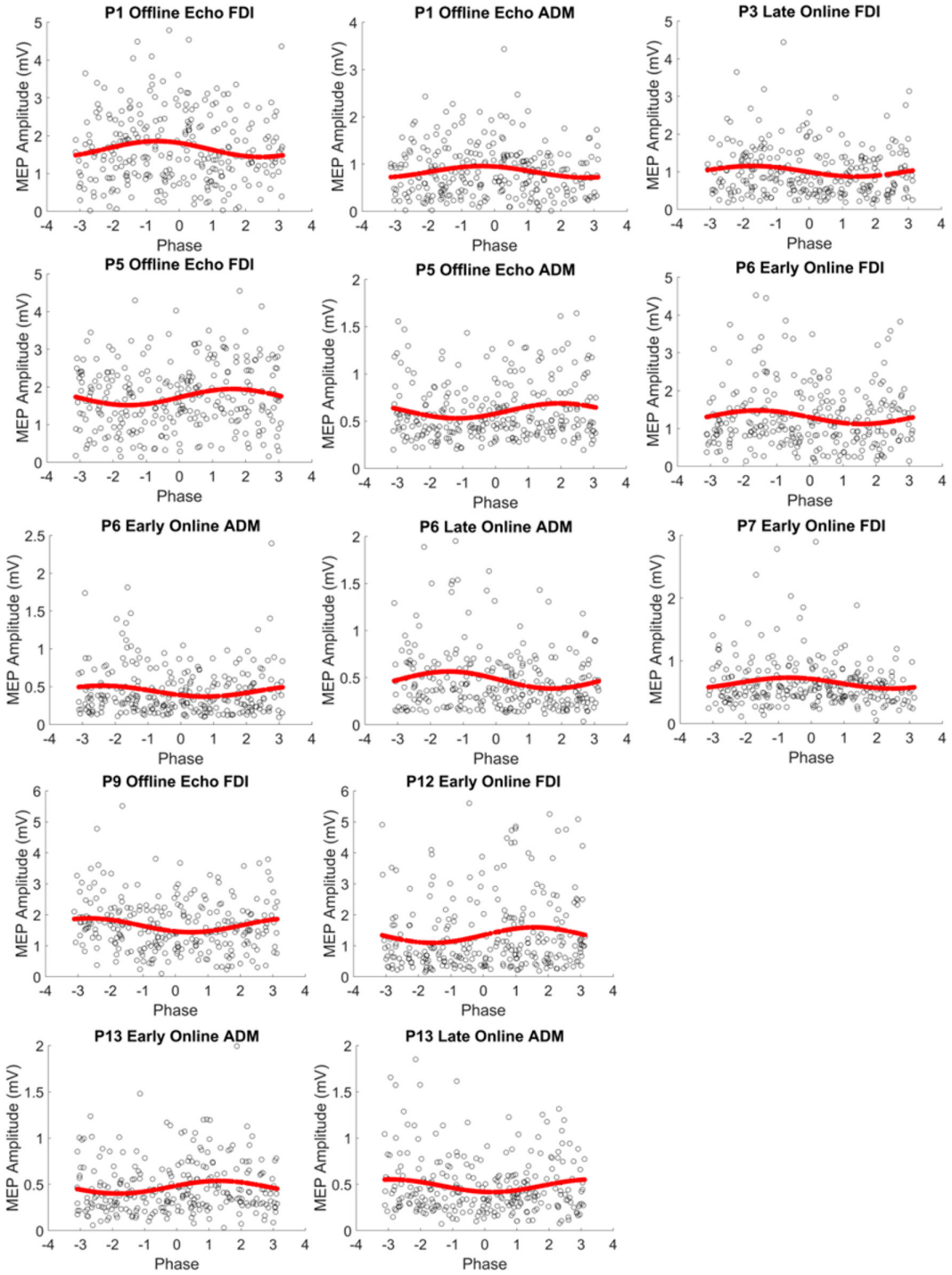

FIGURE 2 | Participant's fitted sinusoidal models with significant entrainment to tACS phase. For each plot, markers represent the observed MEP amplitudes for the participant (e.g., P1 denotes Participant 1), epoch (early online, late online or offline echo) and muscle (FDI or ADM) denoted above the plot (~270 MEPs across three sessions) sorted according to tACS phase. A phase value of 0 denotes the tACS peak, π or $-\pi$ denotes the trough, $\pi/2$ denotes the falling edge and $-\pi/2$ denotes the rising edge. Red lines represent the fitted sinusoidal models for these MEPs, which had greater amplitudes than the fitted sinusoidal models for at least 950 out of 1000 permutations of the MEPs (i.e., $p < 0.05$).

3.1.2 | Nontarget Muscle (ADM) MEP Amplitudes

As shown in Table 1B, Participants 6 and 13 showed significant phasic entrainment of ADM MEP amplitudes for both early and late online MEPs, whereas Participants 1 and 5 showed significant entrainment for the offline echo MEPs. Similar to the FDI, the group analysis for the ADM revealed significant entrainment for the offline echo MEPs ($p = 0.023$). Furthermore, there was also significant entrainment for the late (but not early) online MEPs ($p = 0.046$).

3.2 | Aftereffects of μ-tACS on MEP Amplitude

As shown in Figure 3, MEP amplitudes were significantly greater post-tACS compared with pre-tACS for both the FDI

TABLE 1 | Table of individual and group *p*-values for permutation analysis of phasic tACS effects on FDI (A) and ADM (B) MEP amplitude.

(A) FDI MEP permutation analysis			
Participant	**Early online *p*-value**	**Late online *p*-value**	**Offline echo *p*-value**
1	0.412	0.502	0.036*
2	0.628	0.473	0.295
3	0.118	0.046*	0.110
4	0.653	0.716	0.908
5	0.534	0.982	0.015*
6	0.042*	0.649	0.579
7	0.029*	0.105	0.444
8	0.666	0.350	0.913
9	0.664	0.645	0.008**
10	0.877	0.156	0.071
11	0.759	0.212	0.970
12	0.047*	0.643	0.346
13	0.065	0.867	0.828
Group	**0.081**	**0.453**	**0.021***
(B) ADM MEP permutation analysis			
Participant	**Early online *p*-value**	**Late online *p*-value**	**Offline echo *p*-value**
1	0.455	0.352	0.031*
2	0.747	0.561	0.334
3	0.990	0.219	0.320
4	0.825	0.316	0.408
5	0.986	0.828	0.010**
6	0.033*	0.006**	0.825
7	0.136	0.189	0.054
8	0.381	0.188	0.636
9	0.917	0.125	0.493
10	0.783	0.359	0.063
11	0.232	0.690	0.927
12	0.360	0.998	0.063
13	0.023*	0.037*	0.980
Group	**0.337**	**0.046***	**0.023***

Note: *p*-values > 0.05 are denoted by *, whereas *p*-values > 0.01 are denoted by **. (A) Participants 6, 7 and 12 showed significant phasic entrainment of FDI MEP amplitudes for the early online MEPs. Participant 3 showed significant entrainment for the late online MEPs. Participants 1, 5 and 9 showed significant entrainment for the offline echo MEPs. Revealed significant entrainment for the offline echo MEPs ($p = 0.021$) but no entrainment for either of the online MEPs, although the early online MEPs approached significance ($p = 0.081$). (B) Participants 6 and 13 showed significant phasic entrainment of ADM MEP amplitudes for both early and late online MEPs; Participants 1 and 5 showed significant entrainment for the offline echo MEPs. The group analysis revealed significant entrainment for the offline echo MEPs ($p = 0.023$) as well as the late online MEPs ($p = 0.046$) but no entrainment for the early online MEPs. $N = 13$.

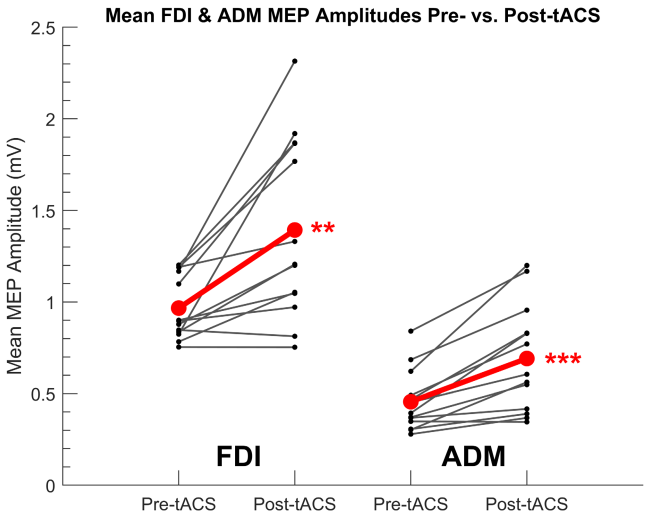

FIGURE 3 | Individual mean FDI (left) and ADM (right) MEP amplitudes before and after μ-tACS. Points represent each participant's mean MEP amplitude from 120 TMS-induced MEPs per participant (40 MEPs per experiment session) acquired before (pre-tACS) and after (post-tACS) receiving 90 'trials' (~36 min) of μ-tACS, with each trial consisting of 16 s of tACS followed by 8 s of rest. Individual differences in mean MEP amplitude are represented by the solid lines. The global mean MEP amplitude for each group is represented by a red point, with the global mean difference from pre- to post-tACS represented by a red line connecting the two red points. A significant increase in MEP amplitude from pre-tACS to post-tACS was reported for both the FDI (two-way rmANOVA: $F_{1,12} = 16.02$, $p_{12} = 0.002$, $\eta^2 = 0.167$; **) and ADM ($F_{1,12} = 27.11$, $p_{12} < 0.001$, $\eta^2 = 0.257$; ***). $N = 13$.

(Left; $\text{mean}_{pre} = 0.97\,\text{mV} \pm 0.17$; $\text{mean}_{post} = 1.39\,\text{mV} \pm 0.5$; $F_{1,12} = 16.02$, $p = 0.002$, $\eta^2 = 0.167$; **) and ADM (Right; $\text{mean}_{pre} = 0.46\,\text{mV} \pm 0.17$; $\text{mean}_{post} = 0.69\,\text{mV} \pm 0.29$; $F_{1,12} = 27.11$, $p < 0.001$, $\eta^2 = 0.257$; ***). Furthermore, there was no main effect of SESSION for either muscle (FDI: $F_{2,24} = 0.884$, $p = 0.426$; ADM: $F_{2,24} = 0.805$, $p = 0.459$) nor were there any STIMULATION × SESSION interactions (FDI: $F_{2,24} = 0.181$, $p = 0.836$; ADM: $F_{2,24} = 0.404$, $p = 0.672$), confirming that there were no significant differences in MEP amplitude between the three sessions.

Mean MEP amplitudes from the offline periods of each block were then compared against each other as well as against the pre- and post-tACS mean amplitudes using a two-way rmANOVA. As shown in Figure 4, there was a significant main effect of TIME for both muscles (FDI: $F_{4,48} = 8.125$, $p < 0.001$, $\eta^2 = 0.115$; ADM: $F_{4,48} = 10.828$, $p < 0.001$, $\eta^2 = 0.144$); however, subsequent post hoc *t*-tests revealed slight differences between the two muscles. The FDI (Figure 4A) showed significant increases in MEP amplitude between the pre-tACS MEPs and the offline MEPs from all three tACS blocks as well as the post-tACS MEPs ($t_{12} = -3.624$, -3.469, -3.753, -4.002; $p = 0.028$, 0.032, 0.025, 0.018; $d = -1.005$, -0.962, -1.041, -1.110 for Blocks 1, 2, 3 and post-tACS, respectively) but no significant differences in MEP amplitude between the three blocks or between any of the tACS blocks and the post-tACS MEPs. This suggests a relatively sharp increase in FDI MEP amplitude within the first tACS block that is then sustained throughout and beyond the stimulation period. Meanwhile,

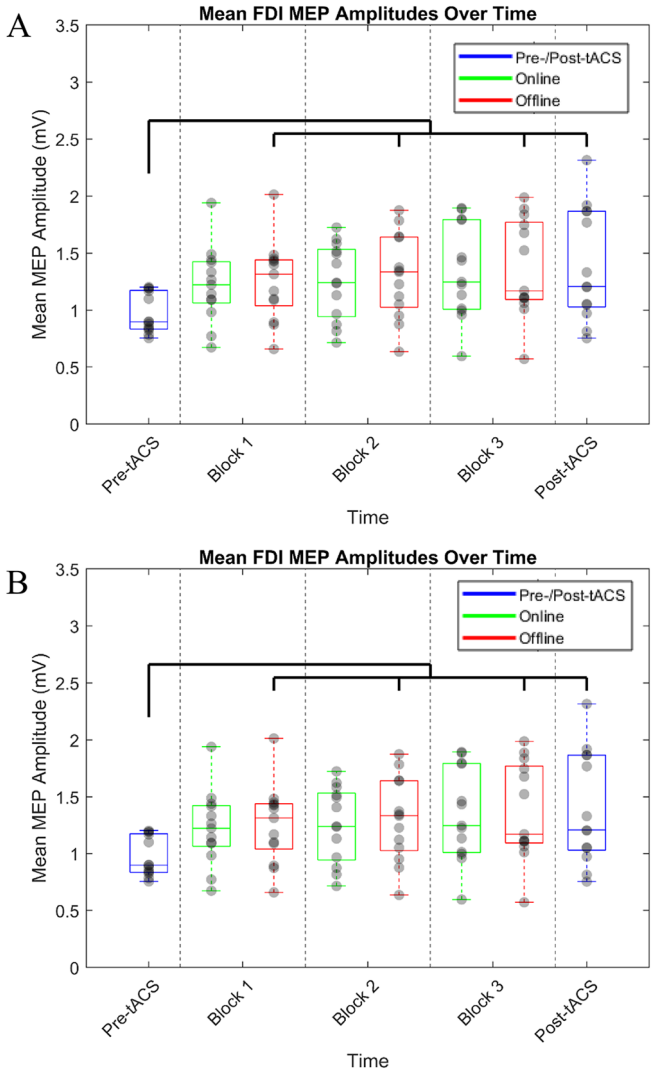

FIGURE 4 | Group FDI (A) and ADM (B) MEP amplitudes before, during and after receiving μ-tACS. Each boxplot represents the participant-mean MEP amplitudes (i.e., the average across the three sessions for each participant) for the time period denoted on the x-axis. The central mark of each boxplot indicates the group median and the bottom and top edges of the boxplot indicate the 25th and 75th percentiles, respectively. The whiskers indicate the most extreme non-outlier values, with outliers indicated by '+'. The blue boxplots represent the MEP amplitudes acquired pre- and post-tACS (120 MEPs per participant across the three sessions). The green boxplots represent MEP amplitudes acquired during the online periods of each block (180 MEPs per participant across the three sessions), whereas the red boxplots represent MEP amplitudes acquired during the offline periods (90 MEPs per participant across the three sessions). (A) There was a significant difference in FDI MEP amplitudes between the pre-tACS MEPs and the offline MEPs from all three tACS blocks as well as the post-tACS MEPs ($t_{12} = -3.624, -3.469, -3.753, -4.002$; $p = 0.028, 0.032, 0.025, 0.018$; $d = -1.005, -0.962, -1.041, -1.110$ for Blocks 1, 2, 3 and post-tACS, respectively; indicated by the solid brackets above the boxplots). (B) There was a significant difference in ADM MEP amplitudes between the pre-tACS MEPs and the offline MEPs from Blocks 2 and 3 as well as the post-tACS MEPs ($t_{12} = -4.231, -5.287, -5.207$; $p = 0.009, 0.002, 0.002$, $d = -1.173, -1.466, -1.444$ for Blocks 2, 3 and post-tACS, respectively) but no significant difference between pre-tACS and Block 1 ($t_{12} = -1.956$; $p = 0.258$). There was also a significant difference in offline MEP amplitude between Block 1 and 2 ($t_{12} = -4.255$; $p = 0.009$; $d = -1.18$; #) but no significant differences between Blocks 1 and 3 ($t_{12} = -3.112$; $p = 0.054$) or Blocks 2 and 3 ($t_{12} = -2.084$; $p = 0.258$). When assessing both the online and offline MEPs of each block, there were significant differences between Block 1 and Blocks 2 and 3 ($t_{12} = -3.928, -3.594$; $p = 0.006, 0.007$; $d = -1.089, -0.997$) as well as a significant difference between Blocks 2 and 3 ($t_{12} = -2.466$; $p = 0.03$; $d = -0.684$). $N = 13$.

the ADM (Figure 4B) showed a significant increase in MEP amplitude between the pre-tACS MEPs and the MEPs from Blocks 2 and 3 as well as the post-tACS MEPs ($t_{12} = -4.231$, -5.287, -5.207; $p = 0.009$, 0.002, 0.002, $d = -1.173$, -1.466, -1.444 for Blocks 2, 3 and post-tACS, respectively) but no significant difference between pre-tACS and Block 1 ($t_{12} = -1.956$; $p = 0.258$). There was, however, a significant increase from Block 1 to Block 2 ($t_{12} = -4.255$; $p = 0.009$; $d = -1.18$) but no significant differences between Blocks 1 and 3 ($t_{12} = -3.112$; $p = 0.054$) or Blocks 2 and 3 ($t_{12} = -2.084$; $p = 0.258$). This suggests a more gradual increase in ADM MEP amplitude compared with FDI MEP amplitude. There were no main effects of SESSION for either muscle (FDI: $F_{2,24} = 1.558$, $p = 0.231$; ADM: $F_{2,24} = 1.246$, $p = 0.306$) nor were there any TIME × SESSION

interactions (FDI: $F_{8,96}=1.247$, $p=0.28$; ADM: $F_{8,96}=1.922$, $p=0.065$), confirming that there were no significant differences in MEP amplitude between the three sessions.

Finally, the online and offline mean MEP amplitudes across each of the three tACS blocks were compared using a three-way rmANOVA. The FDI MEPs showed no main effects of BLOCK ($F_{2,24}=1.741$, $p=0.197$), STIMULATION ($F_{1,12}=2.681$, $p=0.128$) or any BLOCK×STIMULATION interactions ($F_{2,24}=0.125$, $p=0.883$). The ADM MEPs, however, showed a main effect of BLOCK ($F_{2,24}=11.394$; $p<0.001$; $\eta^2=0.073$), with subsequent post hoc *t*-tests confirming significant differences between Block 1 and Blocks 2 and 3 ($t_{12}=-3.928$, -3.594; $p=0.006$, 0.007; $d=-1.089$, -0.997) as well as a significant difference between Blocks 2 and 3 ($t_{12}=-2.466$; $p=0.03$; $d=-0.684$), supporting a gradual build-up in ADM MEP amplitude across blocks. However, similar to the FDI, there was no main effect of STIMULATION, although it was approaching significance ($F_{1,12}=4.287$; $p=0.061$), nor were there any BLOCK×STIMULATION interactions ($F_{2,24}=0.1$, $p=0.905$). There were no main effects of SESSION for either muscle (FDI: $F_{2,24}=1.558$, $p=0.231$; ADM: $F_{2,24}=1.443$, $p=0.256$), although there were significant BLOCK×SESSION interactions for both muscles (FDI: $F_{4,48}=3.075$, $p=0.025$, $\eta^2=0.056$; ADM: $F_{4,48}=3.269$, $p=0.019$, $\eta^2=0.019$). Post hoc *t*-tests showed that the BLOCK×SESSION interaction for the ADM was driven by significant differences between Blocks 1 and 3 for Session 1 ($t_{12}=-4.462$, $p=0.001$) and Session 3 ($t_{12}=-4.779$, $p<0.001$), rather than a significant difference between sessions. However, the driving force for the FDI BLOCK×SESSION interaction could not be elucidated by the post hoc *t*-tests.

3.3 | Aftereffects of μ-tACS on μ/IMF EEG Power

The aftereffects of the tACS paradigm on both μ (8–13 Hz) and IMF (±1 Hz) spectral power were assessed by comparing mean relative EEG powers from the pre-tACS, post-tACS and break periods (5 min each) using a two-way rmANOVA. As shown in Figure 5, there was no significant main effect of TIME for μ power ($F_{3,33}=1.274$, $p=0.299$, $\eta^2=0.046$), although there was a significant TIME*SESSION interaction ($F_{6,66}=2.259$, $p=0.048$, $\eta^2=0.058$). The main effect of TIME for IMF power approached but did not reach significance ($F_{3,33}=2.62$, $p=0.067$, $\eta^2=0.072$). Again, however, there was a significant TIME*SESSION interaction ($F_{6,66}=3.078$, $p=0.01$, $\eta^2=0.081$), with post hoc *t*-tests revealing a significant decrease in IMF power between pre-tACS and Break 2 specifically for Session 1 ($t=3.905$, $p=0.012$, $d=1.139$). There were no main effects of SESSION for μ or IMF ($F_{2,22}=0.225$, 0.155; $p=0.8$, 0.857, respectively).

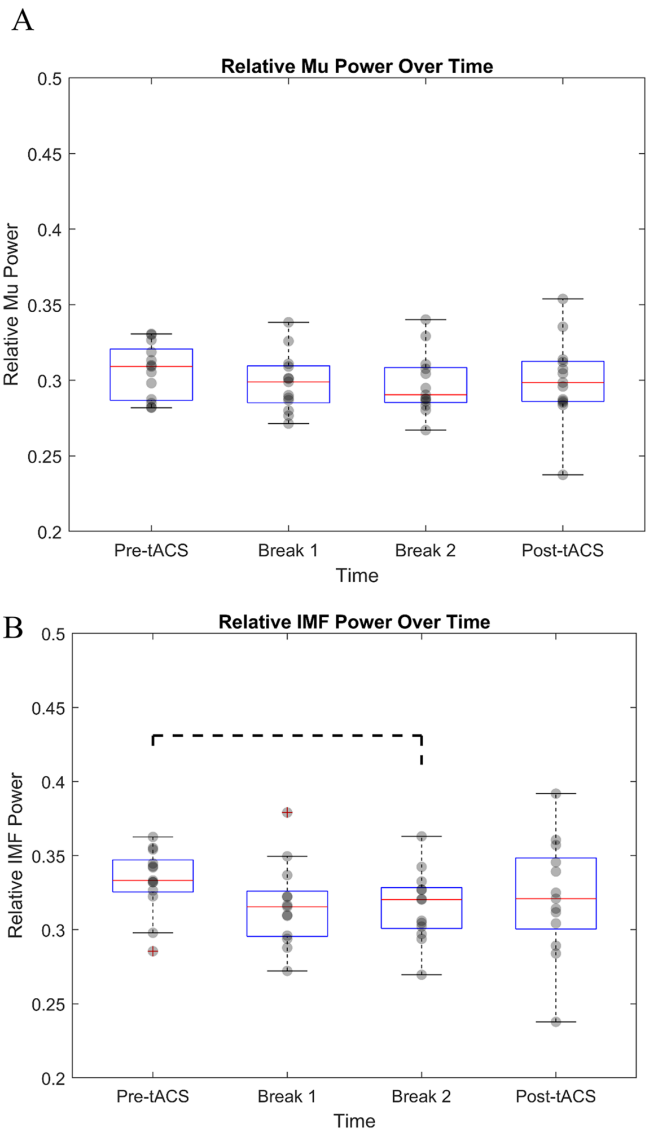

FIGURE 5 | Group Mu (A) and IMF (C) resting EEG powers pre-stimulation, during the break periods and post-Mu-tACS. Each boxplot represents the participant-mean (i.e., the average across the three sessions for each participant) Mu (8–13 Hz) or IMF (±1 Hz) EEG power during 5 min of wake rest. The central mark of each boxplot indicates the group median and the bottom and top edges of the boxplot indicate the 25th and 75th percentiles, respectively. The whiskers indicate the most extreme non-outlier values, with outliers indicated by '+'. (A) There was no main effect of TIME for μ power ($F_{3,33}=1.274$, $p=0.299$, $\eta^2=0.046$), although there was a significant TIME*SESSION interaction ($F_{6,66}=2.259$, $p=0.048$, $\eta^2=0.058$). (B) There was a significant decrease in resting IMF power between pre-tACS and Break 2 but only for Session 1 ($t=3.905$, $d=1.139$, $p=0.012$), indicated by the dashed bracket above the boxplots.

3.4 | Unaffected vs. Affected Sessions

We then performed each of the above analyses separately for the unaffected and affected sessions to assess the importance of precise IMF estimation for inducing entrainment and plastic aftereffects. The main findings of these separate analyses are summarised in Table S1. Regarding the permutation analysis, the unaffected sessions remained significant at the group level for the ADM late online and echo MEPs ($p=0.038$ and 0.005, respectively) and approached significance for the FDI early online and echo MEPs ($p=0.077$ and 0.093, respectively), whereas the affected sessions were only significant for the FDI and ADM late online MEPs ($p=0.013$ and 0.050, respectively) but were not significant for the echo MEPs of

either muscle ($p = 0.250$ and 0.169, respectively). The pre-post increase in MEP amplitude remained significant for the unaffected and affected sessions for both the FDI (unaffected sessions: $t_{11} = -3.038$, $p = 0.011$; affected sessions: $t_9 = -3.516$, $p = 0.007$) and ADM (unaffected sessions: $t_{11} = -3.862$, $p = 0.003$; affected sessions: $t_9 = -4.299$, $p = 0.002$). In fact, the effect sizes were slightly greater for the affected sessions ($d = -1.112$ and -1.36 for the FDI and ADM, respectively) compared with the unaffected sessions ($d = -0.877$ and -1.115, respectively). There were also no major changes in significance when comparing the online and offline MEPs across the tACS blocks. There was, however, a lost main effect of TIME for the affected sessions when comparing the pre-/post-FDI MEP amplitudes against the offline FDI MEPs of each tACS block, although it approached significance ($F_{4,36} = 2.318$, $p = 0.076$, $\eta^2 = 0.205$). There was also a lost main effect of TIME for the affected sessions regarding the changes in resting μ-power, which unlike the lost main effect of TIME for the MEPs, did not approach significance ($F_{3,27} = 0.309$, $p = 0.819$, $\eta^2 = 0.033$).

We also performed correlational analyses comparing the absolute error in frequency targeting against the magnitude of entrainment/plasticity for each individual session. The main findings of these correlational analyses are summarised in Table S2 and Figure S2. These analyses did not reveal any significant correlations between the errors in frequency targeting and the magnitude of any of the tACS effects.

4 | Discussion

Although animal studies (see review by Reato et al. 2013) have provided us with a cursory understanding of how tACS can shift the membrane potentials of pyramidal cells to alter their spike timing in a frequency- and phase-specific manner (Elyamany et al. 2021; Reato et al. 2010), it is less clear how these cellular effects translate into large-scale changes in network activity to induce some of the behavioural and cognitive effects of tACS seen in human studies (for reviews, see Antal and Paulus 2013; Bland and Sale 2019; Herrmann et al. 2016; Vosskuhl, Strüber, and Herrmann 2018; Wischnewski, Alekseichuk, and Opitz 2023). Two primary mechanisms have been proposed thus far: entrainment of endogenous oscillatory activity to the frequency and phase of stimulation (Ali, Sellers, and Frohlich 2013; Helfrich et al. 2014a, 2014b; Huang et al. 2021; Witkowski et al. 2016; Wischnewski et al. 2024) and neuroplastic aftereffects (Kasten, Dowsett, and Herrmann 2016; Neuling, Rach, and Herrmann 2013; Veniero et al. 2015; Vossen, Gross, and Thut 2015; Wischnewski et al. 2019; Wischnewski, Schutter, and Nitsche 2019). The current study aimed to probe both these mechanisms in the context of μ-tACS using both phase-dependent TMS and EEG to assess the phasic (i.e., entrainment) effects on CSE and the sustained (i.e., neuroplastic) aftereffects on CSE and μ power. There was a sustained increase in both FDI and ADM MEP amplitudes as well as preliminary evidence for phasic entrainment of MEP amplitudes persisting briefly poststimulation. There were also decreases in relative μ/IMF EEG power from pre-tACS to the break periods, although there are some limitations to the experimental design that hinder the interpretation of these EEG results.

4.1 | Aftereffects of μ-tACS on CSE

In line with recent μ-tACS studies (Feurra et al. 2019; Fresnoza et al. 2018; Madsen et al. 2019), there were significant increases in mean MEP amplitude from pre- to post-tACS for both the FDI (43.3% increase) and ADM (50% increase), thus supporting a facilitatory effect of μ oscillations on CSE (Bergmann et al. 2019; Karabanov et al. 2021; Ogata et al. 2019; Thies et al. 2018; Wischnewski et al. 2022). The response rate for this facilitatory effect was also highly consistent across participants, with 11 of the 13 participants demonstrating an increase in MEP amplitude (~85% response rate). This is surprising given that many plasticity-inducing paradigms currently in use (e.g., paired-associative stimulation, anodal transcranial direct current stimulation, repetitive TMS and intermittent theta burst stimulation) typically report response rates below 50% (Hamada et al. 2012; López-Alonso et al. 2014; Müller-Dahlhaus et al. 2008; Pellegrini, Zoghi, and Jaberzadeh 2018; Veniero et al. 2015; Wiethoff, Hamada, and Rothwell 2014). Furthermore, contrary to the present study, many studies investigating these paradigms fail to report significant changes in MEP amplitude when the entire participant cohort is analysed (i.e., both responders and nonresponders; for review, see López-Alonso et al. 2014). However, the response rate reported in the present study should also be interpreted with some caution because of the relatively small participant sample size, particularly with regard to the three-way repeated measures ANOVA comparing the online and offline MEP amplitudes across blocks.

It is intriguing that the magnitude of MEP facilitation was similar to that observed in our previous slow-wave (0.75 Hz) tACS study (45.05% increase; Geffen, Bland, and Sale 2021) despite the differences in stimulation frequency. This suggests that plastic aftereffects on CSE may not necessarily be frequency-dependent. Furthermore, tACS in the beta (β) range (15–25 Hz) has also been shown to facilitate resting CSE (Cancelli et al. 2015a,b; Feurra et al. 2011, 2013, 2019; Heise et al. 2016; Wischnewski et al. 2019). However, a meta-analysis by Wischnewski, Schutter, and Nitsche (2019) reported that MEP amplitudes were only increased by β-tACS when using electrode montages with a more posterior location for the return electrode (e.g., M1–Pz or M1–Oz) compared with the M1-supraorbital region montage used in the present study. Therefore, although there may be multiple stimulation frequencies capable of inducing plastic facilitation of CSE, it is still important to consider how the sites of stimulation might impact this effect.

Because the present experiment did not include a negative control stimulation condition (e.g., sham stimulation), changes in MEP amplitude due to other factors (i.e., time and/or arousal effects) technically cannot be excluded. However, it seems highly unlikely that the increases in MEP amplitude reported here would be solely due to time and/or arousal effects, since a meta-analysis by Dissanayaka et al. (2018) found no significant effects of sham stimulation on MEP amplitude compared with baseline across similar time-courses to the current protocol. Although only some of the studies assessed by this meta-analysis investigated tACS specifically, all of the studies used a comparable sham stimulation condition, and thus, they can all be used to make inferences about changes in MEP amplitude solely due to

time and/or arousal. This therefore provides a compelling null comparator for the significant increase in MEP amplitude by μ-tACS.

4.2 | Phasic Effects of μ-tACS on CSE

Although the phasic effects of μ-tACS showed a greater degree of interindividual and intraindividual variability compared with the plastic aftereffects, eight out of 13 participants demonstrated significant entrainment of FDI and/or ADM MEP amplitudes for at least one of the epochs. We also found that the 'preferred phase' of tACS (i.e., the tACS phases that corresponded to the peaks and troughs in MEP amplitudes) varied between participants, potentially due to differences in neuroanatomy (e.g., cortical folding) resulting in varying conduction delays between participants. At the group level, significant entrainment effects were found for the offline echo FDI and ADM MEPs as well as the late online ADM MEPs. Although online entrainment of TMS-evoked potentials has been demonstrated at other tACS frequencies (e.g., Fehér, Nakataki, and Morishima 2017, 2022; Nakazono et al. 2021), to the best of our knowledge, this is the first evidence of phasic entrainment of MEP amplitudes by μ-tACS, contrasting with previous μ-tACS studies that failed to show such an effect of phase on MEP amplitudes (Madsen et al. 2019; Schilberg et al. 2018). Crucially, it is also the first evidence of entrainment echoes for MEP amplitudes occurring *offline* to tACS, building on previous evidence of tACS-induced entrainment echoes for visual perception (van Bree et al. 2021). Together, this evidence suggests that entrainment is not purely an online phenomenon and can indeed persist beyond stimulation. Furthermore, one could also argue that these entrainment echoes are more likely to reflect true entrainment of endogenous oscillations compared with entrainment effects that are observed online to stimulation, for which any observed rhythmic behaviour may simply reflect the rhythmicity of the applied stimulation.

One might traditionally expect the peaks in MEP amplitude to occur around the peaks of the applied tACS (i.e., at instantaneous phase = 0), since at this point the current is travelling from the posterior to the anterior electrode, resulting in anodal (i.e., excitatory) stimulation of M1. Conversely, one would also expect the troughs in MEP amplitude to occur around the troughs of the applied tACS (i.e., at instantaneous phase = $-\pi$ or π), since at this point the current is travelling from the anterior to the posterior electrode, resulting in cathodal (i.e., inhibitory) stimulation of M1. However, this did not appear to be the case in the current data set. Instead, we found that the tACS phases that corresponded with the peaks and troughs in MEP amplitude varied greatly across participants and did not always align with the 'traditional' peaks and troughs of the tACS waveform (see Figure S3). This is likely due to subtle interindividual differences in neuroanatomy (e.g., skull thickness and cortical folding) causing varying conduction delays between participants, as well as many participants not demonstrating strong entrainment to tACS (and thus having a randomly distributed preferred phase).

The interindividual and intraindividual variability observed for these entrainment effects supports the notion that phasic entrainment by tACS is a relatively subtle phenomenon (Kasten et al. 2019; Gundlach et al. 2016; Neuling et al. 2012; Riecke, et al. 2015a,b, 2018; Riecke and Zoefel 2018; Wilsch et al. 2018; Zoefel, Archer-Boyd, and Davis 2018). It thus follows that the inherent trial-to-trial variability of MEP amplitudes (Capaday 2021; Janssens and Sack 2021) would have likely had a greater impact on the power of the phasic analyses compared with the plastic aftereffects. Further, there are a number of uncontrolled factors in the present experiment that may have exacerbated this trial-to-trial variability. This includes physiological factors such as fluctuations in resting EEG activity (Vidaurre, Smith, and Woolrich 2017; Zalesky et al. 2014) or unprovoked motor imagery/activation (Darling, Wolf, and Butler 2006; Gandevia and Rothwell 1987; Hashimoto and Rothwell 1999; Niyazov et al. 2005), as well as methodological factors, such as subtle changes in the position and/or orientation of the TMS coil (Grey and van de Ruit 2017) due to the manual targeting of the M1 hotspot as opposed to more advanced targeting techniques using neuroimaging (e.g., Sparing, Hesse, and Fink 2010; Thielscher et al. 2012). It should be noted, however, that the trial-by-trial variability from these factors would have likely reduced the magnitude of any phasic effects of tACS on MEP amplitude (i.e., they are unlikely to produce a false positive), yet there is evidence supporting entrainment of MEP amplitudes despite this.

It is also worth noting that there is evidence from both animal and human studies suggesting that phasic effects of tACS on the motor system can be induced by *transcutaneous* stimulation of peripheral nerves that then entrain cortical activity, as opposed to direct entrainment of cortical activity via *transcranial* stimulation of the targeted cortical region (Asamoah, Khatoun, and Mc Laughlin 2019). Therefore, it is theoretically possible that the phasic effects on CSE observed in the present study may also be caused by transcutaneous rather than transcranial mechanisms.

4.3 | Aftereffects of μ-tACS on μ/IMF EEG Power

Regarding the aftereffects on EEG power, there was a significant decrease in relative IMF power from pre-tACS to Break 2 specifically for the first experimental session. Although this decrease in spectral power does not align with our hypothesised effects on μ activity, it may instead reflect an acute homeostatic/refractory effect following stimulation (Ketz et al. 2018). This could also explain why it was only observed for the first experiment session, since the participants would likely be desensitised to the stimulation in subsequent sessions. However, there are some limitations to the experimental design that hinder the interpretation of these EEG results, and they should thus be interpreted with a degree of caution.

The first of these limitations is the wakeful rest condition that was used in place of a behavioural test. Although this resting condition was initially chosen to avoid any external influence of a behavioural test on tACS-induced entrainment and/or plasticity, there is growing evidence suggesting that resting brain states can be highly variable both across and within individuals (Vidaurre, Smith, and Woolrich 2017; Zalesky et al. 2014), and thus, changes in EEG power solely due to time cannot be excluded. In fact, a recent functional magnetic resonance imaging (fMRI) study by Meer et al. (2020) characterised 10 distinct

states of cortical activation and found that although resting-state brain dynamics are predominantly bistable between two of these states, the exact brain state dynamics varied significantly both across and within individuals. Importantly, a previous EEG study by Freyer et al. (2009) has suggested that this bistability in resting brain state dynamics reflects non-classic bursting between high- and low-amplitude periods of visual alpha power. Therefore, assuming that resting sensorimotor μ power fluctuates in a similar bistable fashion, any changes in μ power observed in the current study may be driven by these endogenous fluctuations rather than by tACS.

The second limitation hindering the interpretation of the EEG results was the EEG electrode montage used to estimate μ power. A recent study by Karabanov et al. (2021) has suggested that EEG electrode montage may play a crucial role in detecting relationships between μ power and MEP amplitude, reporting a positive correlation between μ power and MEP amplitude when using a Laplacian montage centred around electrode C3 (Thies et al. 2018) that was not present when using radial source projection. Importantly, this Laplacian montage is located posteriorly (i.e., closer to S1) compared with the source projection (i.e., closer to M1). Furthermore, a subsequent study by Zrenner et al. (2022) found that changing the central electrode of the Laplacian montage to one that is closer to M1 can hinder the ability to detect correlations between μ phase and MEP that are present when using a montage centred over S1. Together these findings suggest that μ activity in S1 may be a better predictor of CSE than μ activity in M1. Unfortunately, however, it was not possible to utilise a C3 Laplacian montage in the present study because of the placement of the tACS pad and this would have likely impacted our estimation of μ activity.

4.4 | Impact of Precise IMF Estimation

Because of the errors in IMF estimation that only became apparent post-data collection, some of the sessions had a mismatch between the stimulation frequency (i.e., the initial IMF estimate) and the endogenous eigenfrequency (i.e., the revised IMF estimate). Therefore, we chose to perform separate analyses for the sessions that were affected by these mismatches and the sessions that were unaffected so that we could assess the importance of precise IMF estimation for inducing entrainment and plastic aftereffects. However, it should be noted that any differences in significance (or lack thereof) between the complete analysis and these separate analyses could simply be due to the reduced number of analysed sessions combined with the fact that those sessions had to be averaged for each participant.

The fact that the affected sessions did not show significant entrainment echoes at the group level for either muscle (although they showed significant late online entrainment) suggests that precise IMF estimation may increase the likelihood of inducing entrainment echoes using tACS, in line with the proposed resonance dynamics (i.e., the Arnold tongue) for tACS-induced entrainment (Ali, Sellers, and Frohlich 2013; Huang et al. 2021; Krause et al. 2022; Liu et al. 2018; Schutter and Wischnewski 2016; Thut et al. 2017; Vosskuhl, Strüber, and Herrmann 2018). The changes in relative μ power were also affected by the precision of IMF targeting, with a lost main effect of TIME for the affected sessions. Again, however, these EEG results should be interpreted cautiously because of the limitations discussed in the previous section.

Contrarily, the plastic facilitation of MEP amplitudes did not seem to be significantly impacted by the precision of IMF targeting, in line with previous tACS studies demonstrating similar plastic aftereffects at stimulation frequencies outside the μ frequency band (8–13 Hz), such as slow-wave (0.75 Hz; Geffen, Bland, and Sale 2021) and β-tACS (15–25 Hz; Wischnewski, Schutter, and Nitsche 2019). These findings further support the notion that entrainment and plastic aftereffects are at least partially dissociable (Veniero et al. 2015; Vossen, Gross, and Thut 2015).

Alternatively, the correlational analyses did not reveal any significant relationships between the errors in frequency targeting and the magnitude of entrainment or plastic aftereffects. This would suggest that the accuracy of frequency targeting had little-to-no impact on the effectiveness of the tACS protocol.

5 | Conclusion

To summarise, we present preliminary evidence supporting phasic entrainment of MEP amplitudes persisting beyond stimulation and have also replicated the sustained facilitation of MEP amplitudes observed in previous μ-tACS studies. These findings have important implications in the research and clinical domains as it demonstrates that tACS can effectively modulate neural activity by entraining CSE to match the frequency and phase of stimulation as well as inducing plastic aftereffects on CSE, thus supporting the two primary mechanisms proposed to underlie the behavioural and cognitive effects of tACS. However, the interindividual and intraindividual variability observed for the entrainment effects and the limitations to the EEG analyses warrant further experimentation with improved estimation of endogenous μ activity and a suitable behavioural task to control for differences in resting brain states.

Author Contributions

Asher Geffen: conceptualization, methodology, software, formal analysis, investigation, data curation, writing – original draft, visualisation. **Nicholas Bland:** conceptualization, methodology, software, data curation, writing – review and editing, visualisation, supervision. **Martin V. Sale:** conceptualization, methodology, validation, resources, writing – review and editing, project administration, funding acquisition, supervision.

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Ethics Statement

Ethics approval was granted by The University of Queensland Human Research Ethics Committee in accordance with the National Health and Medical Research Council's guidelines.

Consent

All participants completed a safety screening questionnaire and provided a written statement of informed consent prior to commencing the experiment.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are freely available in the Open Science Framework at 10.17605/OSF.IO/8QY64, reference 'Mu tACS 2021'. The MATLAB scripts used to automatically trigger tACS and TMS as well as the scripts used for statistical analysis are available from the authors upon request.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.