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ABSTRACT

Neural oscillations in the alpha band (7–13 Hz) have long been associated with reductions in attention. However, recent studies have suggested a more nuanced perspective in which alpha oscillations also facilitate processes of cognitive control and perceptual stability. Transcranial alternating current stimulation over occipitoparietal cortex at 10 Hz (alpha-tACS) can selectively enhance EEG alpha power. To assess the contribution of alpha oscillations to attention, we delivered alpha-tACS across four experiments while 178 participants performed sustained attention tasks. Poor performance on all visual tasks was previously associated with increased EEG alpha power. We therefore predicted initially that alpha-tACS would consistently impair visual task performance. However, alpha-tACS was instead found to prevent deteriorations in visual performance that otherwise occurred during sham- and 50 Hz-tACS. This finding was observed in two experiments, using different sustained attention tasks. In a separate experiment, we also found that alpha-tACS limited improvements on a visual task where learning was otherwise observed. Consequently, alpha-tACS appeared to exert a consistently stabilising effect on visual attention. Such effects were not seen in an auditory control task, indicating specificity to the visual domain. We suggest that these results are most consistent with the view that alpha oscillations facilitate processes of top-down control and attentional stability.

Keywords: alpha oscillations, EEG, stabilisation, tACS, visual attention

INTRODUCTION

Electrophysiological recordings of the mammalian brain exhibit robust oscillations during the engagement of multiple, neurocognitive processes (Buzsáki, 2006). Among the most prominent of these oscillations is posterior alpha: a 7 – 13 Hz rhythm recorded most notably at occipitoparietal electrode sites (Berger, 1929). These oscillations (henceforth referred to as 'alpha oscillations') are coordinated by dedicated pacemaker cells in visual thalamus (Lőrincz, Kékesi, Juhász, Crunelli, & Hughes, 2009), are observed across multiple regions of posterior cortex (Hindriks et al., 2015), and have been suggested to reflect an intrinsic rhythm of the human visual system (Hindriks et al., 2015; Rosanova et al., 2009). Consistent with this view, alpha oscillations are strongly linked with changes in visual processing and attention.

In particular, alpha oscillations have been associated with reductions in visual attention (Jensen & Mazaheri, 2010). For example, increases in alpha power are observed during periods of eyes-closed rest (Barry, Clarke, Johnstone, Magee, & Rushby, 2007), and reduced excitability in visual cortex (Romei, Rihs, Brodbeck, & Thut, 2008). Alpha power also increases reliably along with error rates and reaction times during extended cognitive tasks (e.g. Gharagozlou et al., 2015; Schmidt et al., 2009; Wascher et al., 2014), but reduces when motivation is increased via reward (Hughes, Mathan, & Yeung, 2013). Such changes in alpha power closely follow the development of mental fatigue (Boksem, Meijman, & Lorist, 2005; Kecklund & Åkerstedt, 1993) and self-rated attentional focus (Macdonald, Mathan, & Yeung, 2011). Furthermore, over shorter time-scales,

alpha power increases before errors on visual attention tasks (O'Connell et al., 2009), and within regions processing task-irrelevant visual information (Snyder & Foxe, 2010). Such findings have contributed to the established view that alpha oscillations reflect disengagement in visual cortex (Clayton, Yeung, & Cohen Kadosh, 2015). Alpha oscillations have also been suggested to play active roles in suppression of visual processing (Foxe & Snyder, 2011). However, recent studies have begun to question this prevalent view, suggesting that alpha may also contribute positively to many important functions of visual attention (Clayton, Yeung, & Cohen Kadosh, 2017).

For example, alpha oscillations have been reported to facilitate thalamocortical communication (Bastos, Briggs, Alitto, Mangun, & Usrey, 2014; Saalmann, Pinsk, Wang, Li, & Kastner, 2012), to aid signalling of sensory predictions (Mayer, Schwiedrzik, Wibral, Singer, & Melloni, 2015; Sherman, Kanai, Seth, & VanRullen, 2016), and to promote integration within frontoparietal attention networks (Sadaghiani et al., 2012). More generally, although bottom-up transmission of information in visual cortex is thought to occur at higher frequencies, feedback signalling and top-down organisation of visual processing have been linked with alpha oscillations (Bastos et al., 2015; Michalareas et al., 2016; van Kerkoerle et al., 2014). In addition, alpha has been positively associated with stability in visual processing. Decreases in alpha power are observed when people switch their attention between visual tasks (Foxe, Murphy, & De Sanctis, 2014), and immediately before changes in perception of ambiguous visual stimuli (e.g. Necker cubes) (Isoglu-Alkaç et al., 2000; Piantoni, Romeijn, Gomez-Herrero, Van Der Werf, & Van Someren, 2017; Strüber & Herrmann, 2002). Such power

decreases have been suggested to reflect destabilisation of current perceptual interpretations (Piantoni et al., 2017; Strüber & Herrmann, 2002). Consequently, despite clear links with attentional disengagement, a growing body of evidence suggests that alpha oscillations also associate with processes of top-down control and perceptual stability. In this respect, alpha oscillations seem to exhibit an intriguing similarity to the default mode network, whose activity has been associated with mind wandering (e.g. Mason et al., 2007), but also with high levels of sustained, focused attention (e.g. Esterman, Noonan, Rosenberg, & Degutis, 2013).

We investigated this tension in the literature using transcranial alternating current stimulation (tACS). This procedure involves application of oscillating electrical fields to the brain via electrodes positioned on the scalp (Antal & Paulus, 2013; Battleday, Muller, Clayton, & Cohen Kadosh, 2014; Herrmann, Rach, Neuling, & Strüber, 2013). Specifically, we delivered tACS over occipitoparietal cortex at 10 Hz (alpha-tACS) while participants performed sustained attention tasks. This stimulation montage has been found repeatedly to increase the power of posterior alpha oscillations (Helfrich et al., 2014; Neuling, Rach, & Herrmann, 2013; Neuling et al., 2015; Zaehle, Rach, & Herrmann, 2010). Previous electrophysiological studies, while not using tACS, also showed negative associations between alpha power and performance on all visual tasks used in the current study (Chaumon & Busch, 2014; Gonzalez-Rosa et al., 2015; O'Connell et al., 2009). Therefore, our initial prediction was that alpha-tACS would consistently impair performance on all visual tasks. Electroencephalograms (EEG) were recorded before and after the delivery of tACS in all experiments. We expected to

observe consistent increases in EEG alpha power at posterior electrode sites following alpha-tACS. We also anticipated that participants exhibiting the greatest increases in EEG alpha power following alpha-tACS would show the greatest tACS-related impairments in visual task performance.

EXPERIMENT 1

MATERIALS AND METHODS

Participants

Fifty-two healthy adults participated in this first experiment. This sample size was chosen based on the sample sizes of previous studies finding significant, behavioural effects of transcranial stimulation (e.g. Cohen Kadosh, 2013). The sample size was also much greater than previous studies showing modulations of alpha power following alpha-tACS (e.g. Kasten, Dowsett, & Herrmann [2016; n = 17; between-participants design]; Neuling et al. [2013; n = 19 & 22; between-participants design]; Helfrich et al. [2014; n=14; within-participants design]). One participant (in the sham group) was excluded due to excessive EEG noise. Three participants were also excluded because their accuracy on at least one task block was more than 2 standard deviations below mean accuracy on that block across all participants. The final sample therefore consisted of 48 participants (31 females, 6 left-handed, mean age = 22.7, SD = 2.9). All participants gave their written, informed consent before participating. They also completed a safety questionnaire to ensure that they were well hydrated, well slept (> 6 hours sleep), and had not consumed recreational drugs less than 24 hours before participating in the experiment. The study was approved by the UK Ministry of Defence Research Ethics Committee.

General Experimental Design

Task performance was assessed before, during, and after the delivery of tACS. Specifically, we compared the effects of 10 Hz-tACS (alpha-tACS) to sham-

and gamma- (50 Hz) tACS. The control frequency of 50 Hz was chosen as we expected this frequency to have little impact on oscillations in the alpha band. Participants completed 2 sessions of 4 task blocks, with each block lasting 4 minutes and 50 seconds (Figure 1A). Participants were given a fixed-duration break of 40 seconds between blocks. Each session therefore lasted 21 minutes and 20 seconds. EEG was recorded throughout. All participants received alpha-tACS in one of the two sessions. In the other session, participants in the sham control group received sham-tACS, while those in the gamma control group received 50 Hz-tACS (collectively referred to as 'control-tACS'). Participants were randomly assigned to the sham and gamma control groups, and the order of alpha- and control-tACS was counterbalanced across participants. Both the experimenter and participants were blinded to stimulation condition. During alpha- and gamma-tACS, stimulation was applied for 11 minutes from the start of the second block to the start of the fourth block. During sham-tACS, stimulation was applied at 10 Hz during only the first 50 seconds of this period (including ramp-up and down times). All forms of tACS were ramped up over 30 seconds and ramped down over 20 seconds. Alpha- and control-tACS sessions were separated by a break of 25 minutes in which participants watched a nature documentary. Participants were told to relax during this period. This break duration was chosen based on previous pilot data showing that it facilitated good recovery of task performance following fatigue.

All stimuli were presented on a Dell® 23-inch LCD monitor (60 Hz refresh rate) using the Psychophysics Toolbox in MATLAB (Brainard, 1997). The timing of stimulation and EEG recording was controlled using *MatNIC*, which is a toolbox

designed by *Neuroelectrics*® to enable control of tACS and EEG using MATLAB®. The experiment was performed in a well-lit room. Participants practiced the main task before starting the experiment (see details below). tACS electrodes were then positioned using a *Neuroelectrics*® cap.

EEG and Transcranial Alternating Current Stimulation

EEG data were recorded using a *Starstim*® device (Neuroelectrics, Barcelona) with Ag/AgCl coated electrodes (diameter = 12mm, contact area = 1cm^2). These electrodes were placed at PO7, PO8, P3, P4, Fz, and FPz. Two reference electrodes (*Covidien*, H124SG) were positioned on and just below the right mastoid bone. tACS was delivered using the same *Starstim*® device through two 25 cm^2 circular sponge electrodes placed on the scalp, centred at Oz and Cz (Figure 1B). This tACS montage has been found to enhance posterior alpha power when applied at 10 Hz (Helfrich et al., 2014; Neuling et al., 2015). Modelling studies also suggest that this montage directs current flow through occipitoparietal cortex (Neuling, Wagner, Wolters, Zaehle, & Herrmann, 2012). All electrodes were positioned using a *Neuroelectrics*® cap according to the 10-20 system. tACS electrodes were soaked in saline solution and coated with conductive electrolyte gel (*Signagel*®, Parker Laboratories) to ensure good conductivity with the scalp. EEG electrodes were filled with the same conductive gel. Impedance levels of tACS electrodes were measured and, if greater than 5 kΩ, additional conductive gel was injected onto the surface of each electrode. To ensure that stimulation was comfortable for all participants, 20 seconds of tACS was delivered at 10 Hz with a ramp-up time of 30 seconds, first at an amplitude of 1 mA and then, if well-tolerated, at 2 mA peak-to-peak. All participants included in our analyses received

stimulation at 2 mA.

Visual Continuous Temporal Expectancy Task

Participants performed the visual Continuous Temporal Expectancy Task (vCTET), which was adapted from one previously used by O'Connell et al. (2009) and Berry et al. (2014). It was chosen because of its prior use in sustained attention research (Berry et al., 2014; Wilson, Gray, Van Klinken, Kaczmarczyk, & Foxe, 2017), and due to the finding that errors on this task are preceded by significant increases in EEG alpha power (Dockree et al., 2017; O'Connell et al., 2009). This latter finding indicates a negative association between vCTET performance and alpha activity, motivating our prediction that alpha-tACS would impair performance on this task. On every trial of the vCTET, an 8 cm^2 square was presented centrally on a grey background. This square was divided into a 10 x 10 grid of identical square tiles, with each tile diagonally split into black and white halves. These tiles shifted their orientation by 90° in a random direction on every trial. The stimulus was presented for 800 ms on ~91% of trials (300 per block). These were classified as ‘standard trials’. The stimulus was presented for 1070 ms on the other ~9% of trials (30 per block). These were classified as ‘target trials’ (Figure 2A). The order of trials was pseudo-randomised such that between 7 and 15 (mean = 10) standard trials were presented between targets. All trials were preceded by a 20 ms grey-screen interval. Participants were instructed to monitor the length of time each stimulus was presented for and to press the space bar whenever they detected a target trial. Responses were classified as correct if made less than 2.46 seconds (3 trials) after a target trial (Berry et al., 2014). However, while participants were told to maximise their accuracy, they were not

asked to prioritise response speed.

During the practice vCTET, participants were required to identify 6 target trials consecutively without missing any, and without incorrectly classifying any standard trials as targets. We did not collect precise data on how long each participant took to complete this practice task. However, the majority completed it in less than 4 minutes. Following misses, “Target Missed” was presented in red lettering below the next image in the stimulus stream. Following incorrect classifications, “Not a Target” was presented in blue lettering at the same location. When a target was correctly classified, “Correct [n]/6” was presented in green lettering above the next image in the stream (‘n’ indicating how many targets had been consecutively detected so far). Feedback was not given during the main task.

Condition Blinding

tACS can have a number of unwanted effects. These include scalp discomfort and itching, as well as visual disturbances caused by electrical stimulation of the retina (e.g. phosphenes; Schutter, 2016). We therefore sought to confirm that such unwanted effects did not have a significant influence on our results. To do this, we told participants about the common side effects of tACS at the end of their participation, and asked them to state in which of the two tasks sessions they thought these effects were most intense. We calculated the percentage of participants that reported most intense experiences during alpha-tACS and compared this with chance (i.e. 50%) using a binomial test.

Statistical Analyses

EEG analyses

All data analyses were performed using MATLAB®. Spectral power was determined by dividing EEG data into multiple, two-second segments. Bad channels and segments with excessive noise were identified manually and excluded. Power spectra were then calculated for each of these segments using the 'ft_freqanalysis' function of the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2010). Power was estimated for frequencies between 1 and 40 Hz, with a frequency resolution of 0.25 Hz. Multi-tapering, using discrete prolate spheroidal sequences, was applied with 1 Hz spectral smoothing. To determine individualised alpha bands, average power spectra for each participant were calculated from EEG data collected during both task sessions from all posterior electrodes (PO7, PO8, P3, P4). Individual alpha frequencies (IAFs) were then identified by picking the highest peak in the spectrum within an extended alpha band of 6 – 14 Hz (Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014). For participants with identifiable alpha peaks, the alpha band was defined as IAF ± 3 Hz (Franciotti, Brancucci, Della Penna, Onofrj, & Tommasi, 2011; Klimesch, Doppelmayr, Schimke, & Pachinger, 1996). For participants displaying no identifiable alpha peaks (11.4%), a canonical alpha band of 7 – 13 Hz was used. The significance of results and effect sizes was unaffected when these participants were excluded from analyses. We also observed no significant interactions when the detectability of alpha peaks was included as a between-participants factor (identifiable vs. unidentifiable). To determine the effect of tACS on posterior alpha power, we calculated power spectra for the ~5 minutes of EEG data recorded

before and after the delivery of stimulation for each participant. Using the same approach as in previous studies, post-stimulation power spectra were divided by pre-stimulation power spectra to produce a measure of normalised percentage change in EEG power for each participant in each session (e.g. Clayton, Yeung, & Cohen Kadosh, 2018; Kasten et al., 2016; Neuling et al., 2013). Normalising EEG power in this way ensures that group-wide averages are not biased by participants with large baseline power, which can reflect differences between people that are not fundamentally of interest, such as tissue conductivity (Wen & Li, 2006), muscle tension (Goncharova, McFarland, Vaughan, & Wolpaw), body weight (Babiloni et al., 2011), and phase within menstrual cycles (Bazanova, Kondratenko, Kuzminova, Muravlyova, & Petrova, 2014). Once calculated, these percentage change values were submitted to a mixed ANOVA with the within-participants factors of 'stimulation' (alpha- vs. control-tACS) and 'frequency band' (individualised theta, alpha, and low beta). Individualised theta bands were defined as IAF-6 – IAF-3 Hz. Individualised low beta bands were defined as IAF+3 – IAF+6 Hz. In all analyses, 'stimulation order' and 'control group' (sham- vs. gamma-tACS) were included as between-participants factors. EEG data are plotted separately for sham- and gamma-tACS participants, as well as for participants receiving alpha-tACS in the first and second task sessions, in Supplementary Figure 1. Where there were violations of the assumption of sphericity, the Huynh-Feldt correction was applied. In these cases, the corresponding epsilon value (ε) is stated alongside the ANOVA results. To assess whether effects of alpha-tACS on EEG power were influenced by baseline alpha power, we performed an additional analysis in which alpha power following alpha-tACS was normalised to alpha power following control-tACS (i.e. post-alpha-tACS / post-control-tACS), and mean

alpha power before alpha- and control-tACS was calculated (i.e. mean of pre-alpha- and pre-control-tACS). These two variables were then submitted, along with stimulation order, to a regression analysis. However, in all our experiments, no associations were found between baseline alpha power and post-stimulation effects of alpha-tACS ($p>.4$). These results therefore indicate that changes in EEG alpha power following alpha- vs. control-tACS were not influenced with baseline alpha power.

Behavioural analyses

Percentage accuracy and reaction times were averaged for each block in each session. As false alarm rates were close to zero (0.06%; i.e. the rate at which standard trials were incorrectly labelled as targets), we did not analyse task performance using signal detection theoretic measures. This contrasts with conjunction search task performance (i.e. in Experiment 4), in which false alarm rates are generally higher, and which is most commonly assessed using d' rather than percentage accuracy (e.g. Mahayana et al., 2013; Müller, Vellage, Heinze, & Zaehle, 2015; O'Shea, Muggleton, Cowey, & Walsh, 2004). In the current experiment, behavioural data were submitted to a mixed ANOVA with within-participants factors of 'stimulation' (alpha- vs. control-tACS) and 'task block' (1-4). As with our EEG analysis, 'stimulation order' and 'control group' (sham- vs. gamma-tACS) were included as between-participants factors. Behavioural data are plotted separately for sham- and gamma-tACS participants, as well as for participants receiving alpha-tACS in the first and second task sessions, in Supplementary Figures 2 and 3. Where there were violations of the assumption of sphericity, the Huynh-Feldt correction was again applied. To assess effects of

stimulation on changes in performance over time, we used linear regression to find the line of best fit through performance from the start of stimulation to the end of the task (i.e., from block 2 to 4) for each participant in each session (alpha- and control-tACS). We looked at changes in performance from the start of block 2 in order to examine the effects of stimulation (given that stimulation was delivered from the start of block 2). This slopes-based analysis was applied as an exploratory analysis in this first experiment, but as a confirmatory analysis in all subsequent experiments. This approach allowed us to demonstrate replication of our results across the multiple experiments of this study. For completeness, we also report the results of our ANOVA, which examined differences between stimulation conditions, but without modelling task performance in a linear fashion.

Behavioural-EEG regression analyses

In addition, we assessed the association between the behavioural and electrophysiological effects of alpha-tACS. To do this, we first calculated the difference in performance slopes between alpha- and control-tACS (alpha-tACS performance slope minus control-tACS performance slope). This gave us a single measure of the effect of alpha-tACS on performance changes over time for each participant. We next calculated the difference in percentage power change in the alpha band following alpha- vs. control-tACS. This gave us a single measure of the effect of alpha-tACS on alpha power. To determine the association between these two variables, they were then submitted to a linear regression analysis, with our single behavioural measure as the dependent variable and our alpha power measure as the predictor variable.

RESULTS

We focused first on the effects of tACS on EEG power (averaged over electrodes PO7, PO8, P3, and P4, and normalised to pre-stimulation power) in individualised theta, alpha, and low beta bands (Figure 3A). We submitted this data to a mixed ANOVA with the within-participants factors 'stimulation' and 'frequency band', and the between-participants factors 'stimulation order' and 'control group'. We observed significant main effects of stimulation ($F_{(1,44)}$=9.00, p=.004, η^2_p=.170, ANOVA), and frequency band ($F_{(2,88)}$=7.99, p=.001, η^2_p=.154, ANOVA) that were qualified by a significant interaction between stimulation and frequency band ($F_{(2,88)}$=3.17, p=.047, η^2_p=.067, ANOVA). The main effect of frequency band indicated that, regardless of whether participants received alpha- or control-tACS, EEG alpha power increased reliably from the start to the end of each task session (M=114.0%, SD=21.3%, $t_{(47)}$=4.55, p<.001, d=0.66, one-sample t-test [test value = 100%]). This replicates typical findings in sustained attention research (Craig, Tran, Wijesuriya, & Nguyen, 2012; Gharagozlou et al., 2015; Lim, Quevenco, & Kwok, 2013; Schmidt et al., 2009; Wascher et al., 2014). No corresponding increases were consistently observed in the theta band (M=103.1%, SD=16.0%, $t_{(47)}$=1.33, p=.190, d=0.19, one-sample t-test [test value = 100%]) or low beta band (M=103.8%, SD=21.0%, $t_{(47)}$=1.27, p=.211, d=0.18, one-sample t-test [test value = 100%]). The main effect of stimulation, and the interaction with frequency band, indicated that this increase in alpha power was accentuated following alpha-tACS. In line with our predictions, planned comparisons revealed that percentage change in EEG power was indeed greater following alpha- vs. control-tACS in the alpha band (M=15.0%, SD=44.3%, $t_{(47)}$=2.35, p=.023, d=0.34, paired-samples t-test). However, no reliable differences

were observed in the theta (M=5.1%, SD=29.5%, $t_{(47)}$=1.19, p=.240, d=0.17, paired-samples t-test) or low beta bands (M=5.2%, SD=28.2%, $t_{(47)}$=1.27, p=.209, d=0.18, paired-samples t-test). Thus, alpha-tACS exerted a specific, enhancing effect on EEG alpha power. A significant three-way interaction was observed between stimulation, frequency band, and stimulation order ($F_{(2,88)}$=7.64, p=.001, η^2_p=.148, ANOVA). Decomposition of this effect revealed a significant two-way interaction between stimulation and frequency band for participants who received alpha-tACS in the first task session ($F_{(2,40)}$=5.93, p=.006, η^2_p=.229, ANOVA) but not for participants who received alpha-tACS in the second task session ($F_{(2,48)}$=1.07, p=.353, η^2_p=.043, ANOVA). These observations suggest that enhancements in EEG alpha power following alpha-tACS were greater when this stimulation was delivered in the first vs. second task session (Supplementary Figure 1), probably reflecting a state-dependent effect of alpha-tACS (Romei, Thut, & Silvanto, 2016). We observed no significant three-way interaction between stimulation, frequency band, and control group ($F_{(2,88)}$=0.24, p=.786, η^2_p=.005, ANOVA). This finding indicates that the effects of sham- and gamma-tACS on EEG power did not differ from each other reliably.

After confirming that alpha-tACS exerted its predicted influence on brain activity, we next focused on the behavioural effects of this stimulation on vCTET performance. Given that previous vCTET studies have focused primarily on task accuracy (e.g. Berry et al., 2014; O'Connell et al., 2009), we too focused first on accuracy data (Figure 4A). We submitted this data to a mixed ANOVA with the within-participants factors ‘stimulation’ and ‘task block, and the between-participants factors ‘stimulation order’ and ‘control group’. We observed a significant main effect of task block ($F_{(3,132)}$=37.54, p<.001, η^2_p=.460, ε=.819,

ANOVA) with a strong linear trend ($F_{(1,44)}$=59.44, p<.001, η^2_p=.575, ANOVA). This confirms that vCTET accuracy deteriorated steadily over time. We also observed a significant interaction between stimulation and task block ($F_{(3,132)}$=3.20, p=.026, η^2_p=.068, ANOVA). Pairwise comparisons revealed that this interaction was driven by task accuracy being significantly lower in the second task block during alpha- vs. control-tACS sessions (M=-4.4%, SD=13.6%, t(47)=-2.22, p=.031, d=-0.32, paired-samples t-test), similar in the third block (M=1.9%, SD=16.9%, t(47)=0.77, p=.446, d=0.11), but numerically higher in the last block (M=3.1%, SD=15.9%, t(47)=1.33, p=.189, d=0.19). Taken together, these observations therefore indicated that alpha-tACS neither consistently improved nor impaired task accuracy, but instead exerted both positive and negative effects on accuracy at different points during task performance. More specifically, these contrasting influences seemed to have the combined effect of flattening the slope of performance changes from the start of stimulation onwards. To characterise this effect, we used linear regression to find the line of best fit through task accuracy from block 2 to 4 for each participant in each session (alpha- and control-tACS). We henceforth refer to these as '*performance slopes*'. A significant, negative performance slope was observed for control-tACS (M=-0.093, SD=0.140, $t_{(47)}$=-4.59, p<.001, d=-0.66, one-sample t-test [test value = 0]), indicating a significant deterioration in task accuracy from block 2 to 4. In contrast, the mean accuracy performance slope for alpha-tACS did not differ significantly from zero (M=-0.024, SD=0.138, $t_{(47)}$=-1.20, p=.235, d=0.17, one-sample t-test [test value = 0]) and, importantly, was less negative than that observed for control-tACS (M=0.069, SD=0.196, $t_{(47)}$ = 2.43, p=.019, d=0.35, paired-samples t-test). These results therefore indicate that, while significant declines in task accuracy were

observed during control-tACS from the start of stimulation onwards, alpha-tACS alleviated such declines. We observed no significant three-way interaction between stimulation, task block, and stimulation order ($F_{(3,132)}$=1.31, p=.273, η^2_p=.029, ANOVA), indicating that the effects of alpha-tACS on vCTET accuracy did not depend on whether this stimulation was delivered in the first or second task session. We also observed no significant three-way interaction between stimulation, task block, and control group ($F_{(3,132)}$=1.26, p=.291, η^2_p=.028, ANOVA), indicating that the effects of sham- and gamma-tACS on vCTET accuracy did not differ from each other reliably. When we assessed the individual difference correlation between this behavioural effect and EEG alpha power enhancement following alpha-tACS, we found no consistent association (β=.100, $F_{(1,47)}$=0.46, p=.499, linear regression).

It is noteworthy that task accuracy was significantly lower during alpha- vs. control-tACS in block 2. This finding raises the question of whether reduced deteriorations in task accuracy during alpha-tACS could have been caused by a floor effect. In other words, deteriorations in performance could have been less pronounced during alpha-tACS simply because task accuracy reached its lowest point during the first five minutes of stimulation, making any further deteriorations in accuracy less likely. However, this was not the case as accuracy in block 2 during alpha-tACS was significantly higher than in block 4 during control-tACS (M=4.5%, SD=13.6%, $t_{(47)}$=2.33, p=.024, d=0.34, paired-samples t-test). This suggests that performance in block 2 did not reach its lowest level and, therefore, that the observed effects of alpha-tACS on behaviour were not the result of a floor effect.

All aforementioned analyses of accuracy were repeated for median reaction times (Supplementary Figure 2B). A significant main effect of block was again observed ($F_{(3,132)}$=9.57, p<.001, η^2_p=.179, ε=.898, ANOVA), with a significant linear trend ($F_{(1,44)}$=10.61, p=.002, η^2_p=.194, ANOVA). This indicates that reaction times increased reliably over time. However, no interaction was observed between stimulation and task block ($F_{(3,132)}$=0.07, p=.976, η^2_p=.002, ε=.958, ANOVA). Performance slopes analysis also revealed that reaction times did not change reliably from block 2 to 4 (p>.1), and that these slopes did not differ between alpha- and control-tACS (p>.5). We therefore conclude that the effects of alpha-tACS on vCTET performance were restricted to task accuracy.

Lastly, we sought to confirm that our results could not be explained by side effects of tACS differing reliably between our stimulation conditions. At the end of the experiment, participants were told about the most common side effects of stimulation (i.e. scalp sessions and phosphenes), and were asked in which task session they thought these subjective effects were most intense. An administrative error meant that responses were lost for 5 participants. However, among the remaining participants (n=43), 46.5% said that the subjective effects of stimulation were more intense during the alpha-tACS session. A binomial test indicated that this proportion was not significantly greater than chance (i.e. 50%; p=.729). We therefore conclude that the subjective effects of stimulation did not differ reliably between alpha- and control-tACS sessions.

DISCUSSION

The most striking result of this experiment was that alpha-tACS exerted a

supportive effect on vCTET accuracy, limiting the slope of performance deteriorations that were otherwise observed during control-tACS. This effect was observed despite the fact that EEG alpha power was selectively enhanced by alpha-tACS in this experiment, and that increases in alpha power have previously been associated with impairments in vCTET performance (Dockree et al., 2017; O'Connell et al., 2009). Given the unexpected nature of this finding, we sought to replicate it using a different visual attention task. A possible explanation for our results was that alpha-tACS exerted a generally enhancing effect on visual attention. However, performance of the vCTET also relies heavily on time perception, and this process has previously been associated with changes in EEG alpha power (Babiloni et al., 2004). Consequently, alpha-tACS could have influenced task performance by affecting time perception abilities rather than attention.

We addressed this possibility in our second experiment by delivering the same stimulation as in Experiment 1 while participants performed a different visual attention task that does not depend on time perception abilities. We chose a visual threshold detection task as poor performance on this task has also been associated with increased posterior alpha power (Chaumon & Busch, 2014). In all other respects, the experimental design and methods were identical to those of Experiment 1.

EXPERIMENT 2

MATERIALS AND METHODS

Participants

Thirty-nine healthy adults took part in this second experiment. Two participants were excluded because their accuracy on at least one task block was more than 2 standard deviations below mean accuracy on that block across all participants. The final sample therefore consisted of 37 participants (20 females, 2 left-handed, mean age = 23.7, SD = 3.5). Consent forms and safety questionnaires were completed in the same way as in Experiment 1.

Visual Threshold Detection Task

In this task, participants had to detect an unpredictable and briefly presented dot stimulus. A small, white fixation cross (6 mm^2) was continuously displayed in the centre of a black screen. Target stimuli consisted of small grey dots (diameter = 1 mm) that appeared with equal frequency for 16.7 ms on either the left or right side of the screen. These dots were presented between two white, vertical lines that were continuously displayed 8.5 cm either side of the central fixation cross (Figure 2B). Participants were instructed to focus on the central cross and respond to the presentation of dot targets as quickly and as accurately as possible by pressing the space bar. Inter-stimulus intervals varied randomly between 2500 and 3500 ms (mean = 3000 ms). Stimulus perceptibility was varied by adjusting stimulus luminance. At the beginning of the experiment, participants completed a single task block in which an adaptive staircase procedure was used

to determine 50% detection thresholds for each participant (Watson & Pelli, 1983). During the main experiment, stimuli were presented with equal frequency at three different luminance levels: 0, 1, and 3 decibels from 50% threshold. Each block consisted of 96 trials. As in Chaumon and Busch (2014), participants performed all sessions of this task in dark conditions. The rest of the methods were identical to those of Experiment 1.

RESULTS

As in Experiment 1, we first examined the effects of stimulation on EEG power (averaged over electrodes PO7, PO8, P3, and P4, and normalised to pre-stimulation power) in individualised theta, alpha, and low beta bands (Figure 3B). We again observed a main effect of frequency band ($F_{(2,66)}$=4.65, p=.018, η^2_p=.124, ε=.843, ANOVA). This effect was driven by significantly increased percentage change in EEG power from pre- to post-stimulation, independent of stimulation condition, in the alpha band (M=108.8%, SD=23.0%, $t_{(36)}$=2.33, p=.026, d=0.38, one-sample t-test [test value = 100%]), but not in the theta (M=102.6%, SD=10.8%, $t_{(36)}$=1.46, p=.154, d=0.24, one-sample t-test) or low beta bands (M=97.9%, SD=12.2%, $t_{(36)}$=-1.03, p=.310, d=-0.17, one-sample t-test). This result indicates again that, regardless of whether participants received alpha- or control-tACS, EEG alpha power increased reliably from the start to the end of each task session, replicating previous studies of sustained attention (Craig et al., 2012; Gharagozlou et al., 2015; Lim et al., 2013; Schmidt et al., 2009; Wascher et al., 2014). However, the predicted interaction between stimulation and frequency band was not found to be significant ($F_{(2,66)}$=1.57, p=.216, η^2_p=.045, ANOVA). Planned comparisons, motivated by our initial predictions and the results of Experiment 1,

revealed that percentage change in EEG power did not differ reliably following alpha- vs. control-tACS in either the theta (M=1.9%, SD=23.9%, $t_{(36)}$=0.48, p=.635, d=0.08 paired-samples t-test), alpha (M=-7.0%, SD=41.0%, $t_{(36)=}$-1.03, p=.309, d=0.17, paired-samples t-test) or low beta bands (M=0.1%, SD=20.9%, $t_{(36)}$=0.04, p=.967, d=0.005, paired-samples t-test). If anything, alpha power was descriptively higher following control- vs. alpha-tACS. Consequently, we conclude that alpha-tACS had no reliable effect on EEG power in the current experiment.

We focused next on behaviour, looking first at task accuracy (Supplementary Figure 2C). A significant main effect of block was again observed ($F_{(3,99)}$=30.58, p<.001, η^2_p=.481, ε=.920, ANOVA) with a strong linear trend ($F_{(1,33)}$=52.18, p<.001, η^2_p=.613, ANOVA), indicating that accuracy decreased reliably over time. However, no significant interaction was observed between task block and stimulation ($F_{(3,99)}$=1.15, p=.332, η^2_p=.034, ANOVA). Performance slopes analysis also revealed that task accuracy did not change significantly from block 2 to 4 during either alpha- (M=-0.039, SD=0.12, $t_{(36)}$=-1.93, p=.062, d=0.32, one-sample t-test [test value = 0]) or control-tACS (M=-0.026, SD=0.14, $t_{(36)}$=-1.11, p=.275, d=-0.18, one-sample t-test), and that these slopes did not differ between stimulation conditions (M=-0.014, SD=0.128, $t_{(36)}$=-0.65, p=.523, d=0.11, paired-samples t-test). We therefore conclude that there was no consistent effect of alpha-tACS on task accuracy in the current experiment.

As with task accuracy, analysis of median reaction times (Figure 4B) also revealed a significant main effect of task block ($F_{(3,99)}$=13.03, p<.001, η^2_p=.283, ε=.644, ANOVA), with a strong linear trend ($F_{(1,33)}$=20.49, p<.001, η^2_p=.383, ANOVA), indicating consistently worsening performance over the course of each

task session. Importantly though, similar to Experiment 1, we observed a marginally significant interaction between stimulation and task block ($F_{(3,99)}$=2.36, p=.084, η^2_p=.067, ε=.884, ANOVA). This suggested an effect of alpha-tACS on block-wise increases in reaction times. Using our previously described slopes analysis to investigate this effect, we observed a significant, positive slope for control-tACS (M=0.022, SD=0.042, $t_{(36)}$=3.15, p=.003, d=0.52, one-sample t-test [test value = 0]), indicating slowing of responses over time. Given that no significant slopes were observed for task accuracy in this experiment, this finding suggests that, in contrast to Experiment 1, reaction times rather than accuracy were most sensitive to deteriorations in visual attention. However, in contrast to performance slopes during control-tACS, the mean slope for alpha-tACS did not differ reliably from zero (M=-0.004, SD=0.045, $t_{(36)}$=-0.53, p=.602, d=0.09, one-sample t-test [test value = 0]) and, importantly, was significantly less positive than that of control-tACS (M=0.026, SD=0.067, $t_{(36)}$=2.36, p=.024, d=0.39, paired-samples t-test). Consequently, while reaction times slowed during control-tACS from the start of stimulation to the end of the task, such deteriorations in performance were not observed during alpha-tACS. This finding therefore suggests that alpha-tACS again exerted a supportive effect on a measure of task performance that was sensitive to deteriorations over time. We observed no significant three-way interaction between stimulation and task block, and either stimulation order ($F_{(3,99)}$=1.06, p=.364, η^2_p=.031, ε=.884, ANOVA), or control group ($F_{(3,99)}$=1.07, p=.361, η^2_p=.031, ε=.884, ANOVA). We also observed no association across participants between this stabilising effect of alpha-tACS on reaction times and changes in EEG alpha power following alpha-tACS (β=.110, $F_{(1,36)}$=0.43, p=.518, linear regression).

Lastly, we again sought to confirm that our results could not be explained by side effects of tACS differing reliably between stimulation conditions. Using the same method as in Experiment 1, 59.5% of participants said that the subjective effects of stimulation were more intense in the alpha-tACS session. A binomial test indicated that this proportion was not significantly greater than chance (i.e. 50%; p=.162). We therefore conclude that, as in Experiment 1, the subjective effects of stimulation did not differ reliably between alpha- and control-tACS sessions.

DISCUSSION

Although we did not observe an effect of alpha-tACS on task accuracy, this second experiment replicated the behavioural results of our first in terms of median reaction times: Whereas reaction times increased naturally during control-tACS, and while poor performance on this task had previously been associated with increased EEG alpha power (Chaumon & Busch, 2014), delivery of alpha-tACS prevented such deteriorations in reaction times from the start of stimulation onwards. It is unclear why this supportive effect of alpha-tACS on task performance was observed in accuracy in the first experiment, but in reaction times in this second experiment. This issue of behavioural effects being differently expressed in different measures of cognitive performance is a long-standing issue in psychology (Pachella, 1973). One possibility is that, as performance slopes for task accuracy (from block 2 to 4) did not differ reliably from zero across stimulation conditions in this second experiment, it was unlikely that alpha-tACS would have exerted a stabilising influence on them. Of relevance to this point, reaction time performance slopes also did not differ from zero in Experiment 1 and were similarly unaffected by alpha-tACS.

Given such considerations, it seems that this second experiment provides a conceptual replication of our first experiment. In measures of task performance that were sensitive to deteriorations in attention over time, alpha-tACS appeared to limit the slope of such deteriorations. Furthermore, given the significant differences between the tasks used in these two experiments, the current results suggest that the behavioural effects of alpha-tACS are generalisable across different domains of visual attention. The remaining question was therefore why alpha-tACS would exert such generalisable effects on visual attention task performance. One possibility is that alpha-tACS influences processes in the brain that are dedicated to visual processing and attention. However, alternatively, alpha-tACS could exert generalised, modality-independent effects on cognitive processing (e.g. changes in arousal; Mauri, Miniussi, Balconi, & Brignani, 2015). We sought to answer this question in Experiment 3 by delivering the same stimulation as in our two previous experiments while participants performed an auditory version of the Continuous Temporal Expectancy Task (aCTET). In other words, participants performed an auditory version of the task used in Experiment 1. If the effects of alpha-tACS were specific to the visual domain, we would not expect to replicate our previous behavioural results in this experiment. However, if modality-independent mechanisms mediated the behavioural effects of alpha-tACS, we would expect to observe similar protections of auditory task performance from deteriorations over time.

EXPERIMENT 3

MATERIALS AND METHODS

Participants

Forty-four healthy adults took part in this third experiment. Three participants were excluded because their accuracy on at least one task block was more than 2 standard deviations below mean accuracy on that block across all participants. The final sample therefore consisted of 41 participants (26 females, 7 left-handed, mean age = 23.2, SD = 2.7).

Auditory Continuous Temporal Expectancy Task

Participants performed an auditory version of the Continuous Temporal Expectancy Task (aCTET), in which they had to detect when an auditory stimulus had been played for longer than usual. This task was adapted from one previously used by Berry et al. (2014) and was chosen to enable both the study of auditory attention and comparability with the results of the vCTET task in Experiment 1. On each trial, an auditory stimulus was played through in-ear headphones. Each stimulus consisted of two, simultaneously played square wave tones, one at 220 Hz and the other at 329.63 Hz. This stimulus was presented for 800 ms on ~91% of trials ('standard trials'; 300 per block) and 1000 ms on the other ~9% of trials ('target trials'; 30 per block) (Figure 2C). A reduced target duration of 1000 ms (with respect to Experiment 1) was chosen with the aim of ensuring that task difficulty in the aCTET was approximately equivalent to that of the vCTET. Berry et al. (2014) had previously observed significantly better performance on the aCTET vs. vCTET when target durations were fixed at 1070 ms. Throughout task

performance, a constantly displayed message told participants to keep their eyes open and focused on the screen. As in the vCTET, the order of trials was pseudo-randomised such that between 7 and 15 (mean = 10) standard trials were presented between targets. All trials were preceded by a 20 ms period of silence. The aim of the task was to assess the length of time each tone was played for and to press the space bar whenever a longer, 'target' trial was heard. Responses were classified as correct if made less than 2.46 seconds (3 trials) after a target presentation (Berry et al., 2014). However, participants were again not asked to prioritise response speed, but were told to maximise their accuracy. As in Experiment 1, participants completed a practice session of this aCTET in which they had to identify 6 target trials consecutively without missing any, and without incorrectly classifying any standard trials as targets. Feedback was given during this practice as in Experiment 1, but was not given during the main task. The rest of the methods were identical to those of Experiment 1.

RESULTS

As in our previous experiments, we focused first on EEG results (Figure 3C). However, we observed no significant main effects of either frequency band ($F_{(2,74)}$=1.50, p=.231, η^2_p=.039, ANOVA) or stimulation ($F_{(1,37)}$=0.08, p=.779, η^2_p=.002, ANOVA). We also observed no reliable interaction between stimulation and frequency band ($F_{(2,74)}$=0.15, p=.865, η^2_p=.004, ANOVA). Planned comparisons, motivated by our initial predictions and the results of Experiment 1, revealed that percentage change in EEG power did not differ reliably following alpha- vs. control-tACS in either the theta (M=-3.2%, SD=41.7%, $t_{(40)}$=-0.49, p=.626, paired-samples t-test), alpha (M=0.05%, SD=68.9%, $t_{(40)}$=.005, p=.996,

paired-samples t-test) or low beta bands (M=-3.2%, SD=46.4%, $t_{(40)}$=-0.446, p=.658, paired-samples t-test). Thus, alpha-tACS had no reliable effect on EEG power in the current experiment.

We next focused on task performance, and the effect of alpha-tACS on aCTET accuracy (Figure 4C). As expected, we observed a significant main effect of task block ($F_{(3,111)}$=22.44, p<.001, η^2_p=.377, ε=.806, ANOVA) with a strong linear trend ($F_{(1,37)}$=33.99, p<.001, η^2_p=.479, ANOVA). Slopes analysis revealed that task accuracy declined significantly from block 2 to 4 during both alpha- (M=-0.042, SD=0.117, $t_{(40)}$=-2.32, p=.026, d=-0.36, one-sample t-test [test value = 0]) and control-tACS (M=-0.036, SD=0.110, $t_{(40)}$=-2.11, p=.041, d=-0.33, one-sample t-test). However, in contrast to Experiment 1, we did not observe a significant interaction between stimulation and task block ($F_{(3,111)}$=0.11, p=.95, η^2_p=.003, ANOVA). We also observed no difference in accuracy performance slopes between alpha- and control-tACS (p>.5). This suggests that alpha-tACS had no influence on aCTET accuracy in the current experiment. We then applied the same analyses to median reaction times (Supplementary Figure 3B) and again observed a significant main effect of task block ($F_{(3,111)}$=8.95, p<.001, η^2_p=.195, ε=.868, ANOVA) with a strong linear trend ($F_{(1,37)}$=17.38, p<.001, η^2_p=.320, ANOVA). This indicates that reaction times increased reliably from the start to the end of each task session. However, slopes analysis showed that reaction times did not increase reliably from block 2 to 4 during either alpha- (M=0.006, SD=0.029, $t_{(40)}$=1.29, p=.205, d=0.20, one-sample t-test [test value = 0]) or control-tACS (M=0.006, SD=0.027, $t_{(40)}$=1.38, p=.175, d=0.22, one-sample t-test). We also observed no significant interaction between stimulation and task block

($F_{(3,111)}$=0.04, p=.991, η^2_p=.001, ANOVA), and no significant differences between the reaction time performance slopes of alpha- vs. control-tACS (p>.5). We therefore conclude that, although performance on the aCTET deteriorated reliably over time, alpha-tACS had no reliable influence on these deteriorations.

An important, remaining question was whether the behavioural effects of alpha-tACS were significantly different between visual and auditory versions of the CTET. To enable comparison between experiments, we divided task accuracy performance slopes (from block 2 to 4) during alpha-tACS for each participant by the mean task accuracy performance slope during control-tACS in each experiment. A value of less than one on this measure indicates that the slope of decline during alpha-tACS was less steep than the slope during control-tACS. In other words, a value of less than one indicates reduced deterioration (or stabilisation) in task accuracy during alpha-tACS. We then submitted these normalised slope values to a three-way ANOVA with fixed, between-participants factors of 'sensory modality' (i.e., vCTET vs. aCTET), 'stimulation order', and 'control group'. We observed a trend level main effect of sensory modality ($F_{(1,88)}$=2.96, p=.089, η^2_p=.035, ANOVA), indicating a potential difference in the effects of alpha-tACS on performance deteriorations in our visual and auditory tasks. No higher order interactions reached statistical significance. One sample t-tests revealed that normalised slopes were significantly lower than one in Experiment 1 (vCTET; M=0.259, SD=1.493, $t_{(47)}$=-3.44, p=.001, d=-0.50, one-sample t-test [test value = 1]), but not in Experiment 3 (aCTET; M=1.16, SD=3.207, $t_{(40)}$<1, one-sample t-test [test value = 1]).

Lastly, we again asked whether the subjective effects of stimulation differed

between our stimulation conditions. 60.1% of participants said that these subjective effects of stimulation were more intense during alpha-tACS. A binomial test indicated that this proportion was not significantly greater than chance (i.e. 50%; p=.106). We therefore conclude again that the subjective effects of stimulation did not differ reliably between alpha- and control-tACS sessions.

DISCUSSION

Collectively, the findings of these three experiments indicate that, whereas alpha-tACS over occipitoparietal cortex protects visual attention from deteriorations over time, it does not exert such effects on auditory attention. As we observed no tACS-related modulations of alpha power in the current experiment, it is possible that this null behavioural result reflected a failure of alpha-tACS to influence EEG alpha power. Put simply, it is possible that we found no effect of alpha-tACS on aCTET performance because we also observed no effect on brain activity. Nevertheless, behavioural effects of alpha-tACS were observed in Experiment 2 in the absence of accompanying electrophysiological effects, suggesting that alpha-tACS can influence task performance while leaving EEG unaffected. Moreover, we observed no associations between the behavioural and electrophysiological effects of alpha-tACS in either Experiment 1 or 2. We therefore interpret the results of Experiment 3 as suggesting that alpha-tACS over occipitoparietal cortex influenced visual task performance via changes in visual processing specifically, as opposed to generalised effects on cognition (e.g., changes in arousal). However, the mechanisms by which alpha-tACS influenced visual task performance remained unclear.

Our hypothesis, based on the behavioural results of Experiments 1 and 2, was that alpha-tACS caused generalised improvements in visual attention. This would explain why alpha-tACS prevented deteriorations in visual attention over time. However, if this were the case, we asked how alpha-tACS might influence performance on a visual task in which performance naturally *improved*, rather than deteriorated over time. If alpha-tACS enhances visual attention, we would expect to observe greater improvements in task performance during alpha-tACS. However, if no such effects were observed, or if alpha-tACS even prevented such improvements, this would contradict the hypothesis that alpha-tACS generally enhances visual attention. Indeed, if alpha-tACS did reduce the slope of performance improvements, this could suggest that alpha-tACS limits the slope of *any* change in task performance over time, regardless of the direction of that change. To address this question, we delivered alpha- and control-tACS, as in our previous experiments, while participants performed a visual search task. We chose a visual conjunction search task as learning on this task has been reported widely (Lobley & Walsh, 1998; Sireteanu & Rettenbach, 2000).

EXPERIMENT 4

MATERIALS AND METHODS

Participants and Visual Conjunction Search Task

Forty-three healthy adults took part in this last experiment (27 females, 6 left-handed, mean age = 23.1, SD=3.1). The visual conjunction search task required participants to search for a target object (an orange square) among distractor items that shared common features with the target (blue squares and orange triangles) (Gonzalez-Rosa et al., 2015). On each trial, a 7x7 object array was presented. The orange square target was present in the array on 50% of trials. Each shape had a height and width of 1.5 cm. A black fixation cross was presented for 500 ms before every trial. All stimuli were presented on a white background. Each grid was presented for 3000 ms (Figure 2D). Participants were instructed to press 'M' on the keyboard when they detected an orange square, or 'Z' if they believed that no orange square was present in the grid. Participants were asked to perform this task as quickly and as accurately as possible. The number of orange triangles ('same-colour distractors') in each grid varied on every trial between 24, 33, or 42. Each distractor ratio was presented with equal frequency. Each block consisted of 84 trials.

During the practice task, participants performed 60 trials of this task. During the first 30 trials, the number of same-colour distractors increased by one with every trial (i.e. one distractor on trial 1, two distractors on trial 2, etc.). From the 31st trial to the end of the practice task, the number of same-colour distractors in each grid varied randomly between 24, 33, and 42 (as in the main experiment).

Feedback was given after every trial of this practice period, but was not given during the main task. Reaction times were calculated from hit and correct rejection trials (i.e. correct trials only). In addition to reaction times, participant sensitivity to target presence was measured using the signal detection theoretic measure d'. This approach follows that of previous studies in this field assessing conjunction search task performance (e.g. Mahayana et al., 2013; Muggleton, Cowey, & Walsh, 2008; Müller et al., 2015; O'Shea et al., 2004). To calculate d' values, '*hit rates*' were extracted for each block, defined as the percentage of trials in each block correctly classified as containing a target. '*False alarm rates*' were also extracted, defined as the percentage of trials in each block that were incorrectly classified as containing a target. Both hit and false alarm rates were then submitted to the *dprime_simple()* function in MATLAB (Cox, 2014). Positive d' values indicate increased sensitivity to target presence. The rest of the methods were identical to those of Experiment 1.

RESULTS

Analysis of the effects of stimulation on EEG power (Figure 3D) revealed a significant main effect of stimulation ($F_{(1,39)}$=4.109, p=.050, η^2_p=.095, ANOVA), with greater percentage change from pre- to post-stimulation in broadband EEG power (theta-low beta) following alpha- vs. control-tACS (105.7% vs. 99.8%, respectively). We also observed a significant main effect of frequency band ($F_{(2,78)}$=17.04, p<.001, η^2_p=.304, ANOVA). This effect was driven by a significantly increased percentage change in EEG power, independent of stimulation condition, in the alpha band (M=111.7%, SD=18.9%, $t_{(42)}$=4.06, p<.001, d=0.62, one-sample t-test [test value = 100%]), that was not observed in the theta (M=97.2%,

SD=9.6%, $t_{(42)}$=-1.92, p=.062, d=-0.29, one-sample t-test) or low beta bands (M=99.3%, SD=10.2%, $t_{(42)}$=-0.464, p=.645, d=-0.07, one-sample t-test). This again indicates that, regardless of whether participants received alpha- or control-tACS, EEG alpha power increased reliably from the start to the end of each task session. Although the interaction between stimulation and frequency band did not reach significance ($F_{(2,78)}$=1.97, p=.146, η^2_p=.048, ANOVA), planned comparisons motivated by our initial predictions and the results of Experiment 1 revealed that percentage change in EEG power was significantly greater following alpha- vs. control-tACS in the alpha band (M=9.9%, SD=30.4%, $t_{(42)}$=2.14, p=.038, d=0.33 paired-samples t-test). However, no reliable differences were observed in the theta (M=4.2%, SD=17.5%, $t_{(42)}$=1.61, p=.115, d=0.25, paired-samples t-test) or low beta bands (M=4.0%, SD=21.3%, $t_{(42)}$=1.22, p=.229, d=0.19, paired-samples t-test). Collectively, these analyses indicate that EEG alpha power was significantly increased following alpha- vs. control-tACS, but that these increases were not significantly greater than those observed in the theta or low beta bands. A significant three-way interaction was observed between stimulation, frequency band, and stimulation order ($F_{(2,78)}$=17.06, p<.001, η^2_p=.304, ANOVA), indicating that alpha enhancement was greater when alpha-tACS was delivered in the first vs. second task session (Supplementary Figure 1). This interaction is similar to the one observed in Experiment 1. Nevertheless, decomposition of this interaction revealed significant two-way interactions between stimulation and frequency band for participants who received alpha-tACS in both the first ($F_{(2,40)}$=10.16, p<.001, η^2_p=.337, ANOVA) and second sessions ($F_{(2,38)}$=8.65, p=.001, η^2_p=.313, ANOVA). Further decomposition showed that, when alpha-tACS was delivered in the first session, the interaction was driven by power increases following alpha-tACS in the

alpha (M=23.3%, SD=30.6%, $t_{(21)}$=3.57, p=.002, d=0.76, paired-samples t-test) and low beta bands (M=7.4%, SD=16.2%, $t_{(21)}$=2.14, p=.044, d=0.46, paired-samples t-test). However, when alpha-tACS was delivered in the second session, the interaction was driven by power increases following alpha-tACS in the theta band (M=9.6%, SD=16.7%, $t_{(20)}$=2.64, p=.016, d=0.58, paired-samples t-test). We observed no significant three-way interaction between stimulation, frequency band, and control group ($F_{(2,78)}$=0.16, p=.855, η^2_p=.004, ANOVA), indicating that the effects of sham- and gamma-tACS on EEG power did not differ from each other reliably.

Following these electrophysiological analyses, we next focused on the effects of alpha-tACS on task performance (Figure 4D). We quantified task accuracy using the signal-detection theoretic measure d', as in previous visual search experiments (e.g. Muggleton, Kalla, Juan, & Walsh, 2011). The d' measure is a composite of both target identification rate and correct rejection rate. We observed a significant main effect of task block ($F_{(3,117)}$=12.73, p<.001, η^2_p=.246, ε=.923, ANOVA) with a strong linear trend ($F_{(1,39)}$=21.60, p<.001, η^2_p=.356, ANOVA). This indicates that d' improved steadily and reliably over time. Importantly, as in Experiments 1 and 2, we also observed a significant interaction between stimulation and task block ($F_{(3,117)}$=2.71, p=.048, η^2_p=.065, ANOVA), confirming an effect of alpha-tACS on changes in d' over time. To investigate this effect further, we again used the linear regression analysis from Experiment 1 to find the line of best fit through d' values from the start of stimulation to the end of the task (i.e. from block 2 to 4). A significant positive slope was observed for control-tACS (M=0.042, SD=0.063, $t_{(42)}$=4.36, p<.001, d=0.67, one-sample t-test [test value = 0]), indicating an improvement in task performance over time.

However, in contrast, the mean slope for alpha-tACS did not differ significantly from zero (M=0.01, SD=0.098, $t_{(42)}$=0.17, p=.867, d=0.10, one-sample t-test [test value = 0]). Furthermore, importantly, this slope was significantly less positive than that observed for control-tACS (M=-0.041, SD=0.118, $t_{(42)}$=-2.29, p=.027, d=0.35, paired-samples t-test). These results therefore indicate that the significant improvements in task performance during control-tACS from the start of stimulation onwards were reduced by alpha-tACS. We again found no association across participants between the effect of alpha-tACS on performance slopes and changes in EEG alpha power (β=-.041, $F_{(1,42)}$=0.07, p=.794, linear regression).

All aforementioned analyses were also conducted on median reaction times (Supplementary Figure 3D). A significant main effect of block was again observed ($F_{(3,117)}$=88.29, p<.001, η^2_p=.694, ε=.908, ANOVA) with a strong linear trend ($F_{(1,39)}$=221.01, p<.001, η^2_p=.850, ANOVA). Slopes analysis revealed that reaction times decreased significantly from block 2 to 4 during both alpha- (M=-0.052, SD=0.052, $t_{(42)}$=-6.53, p<.001, d=-0.99, one-sample t-test [test value = 0]) and control-tACS (M=-0.034, SD=0.052, $t_{(42)}$=-4.31, p<.001, d=-0.66, one-sample t-test). However, no interaction was observed between stimulation and task block ($F_{(3,117)}$=1.33, p=.270, η^2_p=.033, ε=.876, ANOVA). We also observed no difference in reaction time performance slopes between alpha- and control-tACS (M=-0.018, SD=0.082, $t_{(42)}$=-1.42, p=.163, d=-0.216, one-sample t-test [test value = 0]). The effects of alpha-tACS on visual conjunction search task performance were therefore limited to d'.

Lastly, we again asked whether the subjective effects of stimulation differed

between our stimulation conditions. 46.5% said that these subjective effects were more intense in the alpha-tACS session. A binomial test indicated that this proportion was not significantly greater than chance (i.e. 50%; p=.729). We therefore conclude again that the subjective effects of stimulation did not differ reliably between alpha- and control-tACS sessions.

GENERAL DISCUSSION

We delivered tACS over occipitoparietal cortex and recorded its effects on both EEG activity and attention task performance across four experiments. Poor performance on all visual tasks had previously been associated with increased EEG alpha power (Chaumon & Busch, 2014; Gonzalez-Rosa et al., 2015; O'Connell et al., 2009). Furthermore, in all visual experiments, alpha power increased reliably from the start to the end of each task session, regardless of stimulation condition. This is consistent with previous reports of increased EEG alpha power during periods of increased fatigue (Boksem et al., 2005; Craig et al., 2012; Gharagozlou et al., 2015; Kecklund & Åkerstedt, 1993; Lim et al., 2013; Schmidt et al., 2009; Wascher et al., 2014). Nevertheless, despite these negative associations between alpha oscillations and visual attention, we found no evidence that alpha-tACS consistently impaired visual task performance. Instead, across two visual attention tasks in which performance deteriorated naturally over time, alpha-tACS was found to reduce the slope of such deteriorations. Conversely, in a visual search task in which performance naturally improved over time, alpha-tACS flattened the slope of these improvements. Therefore, rather than having a universally negative or positive impact, alpha-tACS appeared to exert a consistently stabilising effect on visual attention task performance.

This stabilising effect was not observed in consistent measures of task performance across experiments, with alpha-tACS stabilising performance accuracy in Experiments 1 and 4, but reaction times in Experiment 2. Observing similar cognitive effects in different measures of task performance has a long history in psychology (Pachella, 1973). The heterogeneity in our results between

task measures is likely due to the heterogeneity of tasks and instructions used across our experiments. Furthermore, deteriorations in performance from the start of stimulation onwards were not always observed in both speed and accuracy measures. For example, negative performance slopes during control-tACS were only observed in task accuracy and reaction times in Experiments 1 and 2, respectively, and it was only in these measures that performance was affected by alpha-tACS. Consequently, it may be that alpha-tACS was only able to stabilise performance in task measures that exhibited a natural deterioration from the start of control-tACS onwards, and that were therefore sensitive to these kinds of declines. It should be noted that, in Experiment 4, both RTs and accuracy (d') decreased significantly over time, but only accuracy was consistently affected by alpha-tACS. This finding therefore conflicts with the previously stated hypothesis. Nevertheless, looking more broadly at the results of this study, effects of alpha-tACS were still observed in 3 of the 4 task measures that showed sensitivity to deteriorations in attention over time. Consequently, the aforementioned hypothesis seems to have at least some explanatory power. Importantly, alpha-tACS over occipitoparietal cortex had no impact on speed or accuracy in an auditory control task, indicating the potential specificity of the effects of alpha-tACS to the visual domain. Furthermore, in our EEG analyses, the influence of alpha-tACS on alpha power was found to be similarly context-dependent, with increases in alpha power following alpha-tACS observed only in Experiments 1 and, to a lesser extent, 4. We also found no evidence of an association across participants between the magnitudes of the behavioural and electrophysiological effects of alpha-tACS.

At the start of this study, we predicted that alpha-tACS would consistently

impair visual task performance. However, our findings did not support this prediction. Therefore, if alpha-tACS does not influence cognition via suppression of visual attention, by what other mechanisms could alpha-tACS have exerted its effects? Our results suggest against the involvement of certain mechanisms. For example, because alpha-tACS was found to influence performance in a consistent manner across three different visual tasks, its effects cannot be task-specific. Furthermore, because our behavioural effects were observed only in visual tasks, and as no differences were observed in the subjective experiences of alpha- vs. control-tACS, our results most likely do not represent general effects of electrical stimulation (e.g. phosphenes, or changes in arousal; Mauri et al., 2015; Schutter, 2016). In addition, our results are not easily explained by mechanisms like homeostatic responses to stimulation. For example, if the supportive effect of alpha-tACS on task accuracy in Experiment 1 was caused by homeostatic overcompensation to the initially impairing effects of alpha-tACS in block 2 (see Figure 4A), we should not have replicated this supportive effect in Experiment 2 (in which no such initial impairments in performance were observed). Additionally, supplementary analyses of event-related potential data revealed no consistent differences between stimulation conditions in the reactivity of visual cortex to visual stimuli across our experiments (Supplementary Figure 4). This finding suggests that alpha-tACS does not exert its effects via simple modulations of sensory cortex excitability. Furthermore, because we observed no reliable differences between the neural or behavioural effects of sham- and 50 Hz-tACS (Supplementary Figures 1-3), our results appear to reflect the specific consequences of alpha stimulation. The central question posed by these results is, therefore, why alpha-tACS specifically would exert such stabilising effects on visual attention task

performance.

As described in the introduction, despite the consistent association between alpha oscillations and reduced visual attention, recent studies have also suggested that alpha may play important roles in visual processing (Clayton et al., 2017). For example, alpha oscillations have been suggested to facilitate communication of feedback signals in the brain (Michalareas et al., 2016; van Kerkoerle et al., 2014). It is therefore possible that alpha-tACS influenced task performance in our experiments by affecting top-down processes in visual cortex. Such processes are known to be highly dynamic. Patterns of neural activity thought to reflect the engagement of top-down control have complex spatiotemporal profiles (Oehrn et al., 2014). Similarly, while neural oscillations are often modelled as regular sinusoids, they are commonly observed only as short bursts in raw recordings (Jones, 2016; Simon et al., 2011). This contrasts with alpha-tACS, which is delivered with a highly regular structure, for a sustained period of time, and often with no correspondence to the events of cognitive tasks being performed (e.g. alpha-tACS is rarely phase-locked to task cues). Consequently, it is possible that alpha-tACS would exert a disruptive influence on top-down signalling. We would like to suggest that, in theory, such disruption could play a role in the behavioural effects observed in this study.

Although speculative at this point, we suggest that our results could be explained by alpha-tACS reducing the changeability of visual attention by interfering with top-down signals that aim to adjust visual attention over time. In order to protect task performance from deteriorations, it is important that attention does not shift away from on-going, task-relevant processes (Clayton et al., 2015).

However, contrastingly, in order to improve visual task performance over time, it is important that visual attention is continuously adjusted in response to task demands (Law & Gold, 2009). Put simply, to maintain one's task performance, it is necessary to maintain one's cognitive state. However, to *improve* one's task performance, it is necessary to *change* one's cognitive state. If internal commands to switch visual attention away from the current task were disrupted by alpha-tACS due to disruption of top-down signals in posterior cortex, this could have made it more likely for attention, and therefore task performance, to remain unchanged over time. This might explain why alpha-tACS reduced the slope of task performance deteriorations in Experiments 1 and 2. Conversely, if internal commands to focus and reorient visual attention were disrupted by alpha-tACS, it is likely that learning, and therefore improvements in task performance, would be equally restricted. This would therefore also account for why alpha-tACS prevented improvements in task performance in Experiment 4. Future experiments could examine the merits of this theory by recording the neural effects of alpha-tACS using imaging methods that enable measurement of brain activity at higher spatial resolutions (e.g. magnetoencephalography and functional magnetic resonance imaging). Future experiments should also assess the effects of alpha-tACS over non-posterior brain regions (e.g. frontal cortex) to understand whether the results of this study reflect the specific consequences of occipitoparietal tACS. Such experiments could determine which areas of the brain are maximally affected by alpha-tACS. More specifically, neuroimaging studies could also assess whether the behavioural effects of alpha-tACS observed in this study relate to changes in functional connectivity within brain networks associated with top-down communication to sensory cortices (e.g. fronto-parietal networks).

In addition to behaviour, another important focus of this study was the effects of alpha-tACS on oscillatory EEG activity. Whereas previous studies have reported enhancements of EEG alpha power following alpha-tACS, we replicated this effect only in Experiments 1 and 4. Furthermore, in both of these experiments, alpha power enhancements were mainly observed when alpha-tACS was delivered in the first task session (Supplementary Figure 1). A possible factor contributing to this inconsistency of effects was variability of baseline alpha power across experiments. Previous studies have reported that alpha-tACS enhances endogenous alpha oscillations only when alpha power is low (Alagapan et al., 2016; Neuling et al., 2013). It should be noted that, within each experiment, we found no association between baseline alpha power and the effects of alpha-tACS on EEG. However, when comparing baseline power between experiments, we found that mean alpha power before the delivery of alpha-tACS was significantly lower in experiments where alpha power increased following alpha-tACS (i.e. Experiments 1 & 4) compared to experiments where alpha power was unaffected by stimulation (i.e. Experiments 2 & 3: ($F_{(1,167)}$=14.03, p<.001, η^2_p=.077; ANOVA). Restricting our analysis to visual experiments only, we also found that alpha power before alpha-tACS was significantly lower in Experiment 1 and 4 vs. 2 ($F_{(1,126)}$=6.30, p=.013, η^2_p=.048; ANOVA). Consequently, consistent with previous findings, our results suggest that increases in alpha power following alpha-tACS may be at least partially dependent on low baseline alpha power. However, such increases may not associate with baseline power in a linear fashion.

Another important question posed by this study is why no associations were observed across participants between the behavioural and electrophysiological

effects of alpha-tACS. Although comparable behavioural effects were observed in Experiments 1 and 2, significant increases in alpha power were observed only in Experiment 1. Such findings are not uncommon. For example, in a recent review, the neural and behavioural effects of tACS were found to correlate only in a minority of studies (Veniero, Vossen, Gross, & Thut, 2015). The reasons for such inconsistent associations between such effects may be mundane. Correlations between two noisy indices are likely to be weak. Furthermore, tACS-induced artifacts in EEG make it difficult to record online effects of stimulation (Noury, Hipp, & Siegel, 2016) (although see Neuling, Ruhnau, Weisz, Herrmann, & Demarchi, 2016), meaning that researchers must focus on after-effects of stimulation that may be substantially weaker than, or even opposite to, online effects. In addition though, it could also be that tACS exerts significant, frequency-specific effects on cognition that are independent of its ability to modulate EEG in a lasting, measurable way. This could raise important questions for researchers using tACS to assess the causal roles of oscillations in cognition. Specifically, if tACS at a given frequency is found to influence behaviour, but this behavioural effect occurs independently of changes in brain activity at the frequency of stimulation, this could make it more difficult to infer causal associations between the two (Thut, Schyns, & Gross, 2011).

In conclusion, based on previous evidence linking increased alpha power to failures in sustained attention, we predicted that delivery of alpha-tACS during visual tasks would cause only impairments in performance. Instead, this stimulation procedure was found to exert a consistently stabilising effect on visual attention. This finding was observed across a range of tasks and seems

incompatible with the idea that alpha oscillations primarily reflect processes of attentional inhibition and disengagement. Instead, our results appear more consistent with emerging hypotheses about the positive contributions of alpha oscillations to visual attention, such as their proposed role in top-down control and perceptual stability. More broadly, this study highlights the possibility that, while a neural oscillation may be strongly associated with a specific cognitive function in correlational studies, experimental manipulation of that oscillation may not influence the associated cognitive function in ways that one would predict.

CONTEXT OF RESEARCH

Alpha oscillations are among the most prominent rhythms produced by the mammalian brain. However, despite this predominance, the roles of alpha oscillations in cognition appear varied and complex. Methods of rhythmic brain stimulation have been suggested to help determine the causal contributions of neural oscillations to cognition. In addition, these methods can modulate performance on a range of cognitive tasks. Funded by the UK Defence Science and Technology Laboratory, the current project drew on this theoretical background, aiming to 1) investigate the association between alpha oscillations and visual attention using alpha-tACS, and 2) determine the viability of using alpha-tACS to influence sustained attention in real-world settings. Given the large number of studies showing negative links between alpha power and visual attention, including our own past research (e.g. Hughes et al., 2013; Macdonald et al., 2011), we assumed that alpha-tACS would reliably impair visual task performance. However, we instead observed a pattern of results suggesting that alpha-tACS exerts a consistently stabilising influence on visual attention. These

results seem to contrast with dominant conceptualisations of alpha as a measure of visual disengagement, and instead appear most consistent with recent evidence associating alpha oscillations with stability in visual processing. As such, these findings provide new insights into the likely functions of alpha oscillations. However, they also demonstrate the difficulty of determining the mechanistic involvement of neural oscillations in cognition. Our results show that, although a specific pattern of brain activity may covary with a specific cognitive function, experimental modulation of that brain activity may not influence cognitive functioning in ways that one would expect.

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FIGURES

Figure 1

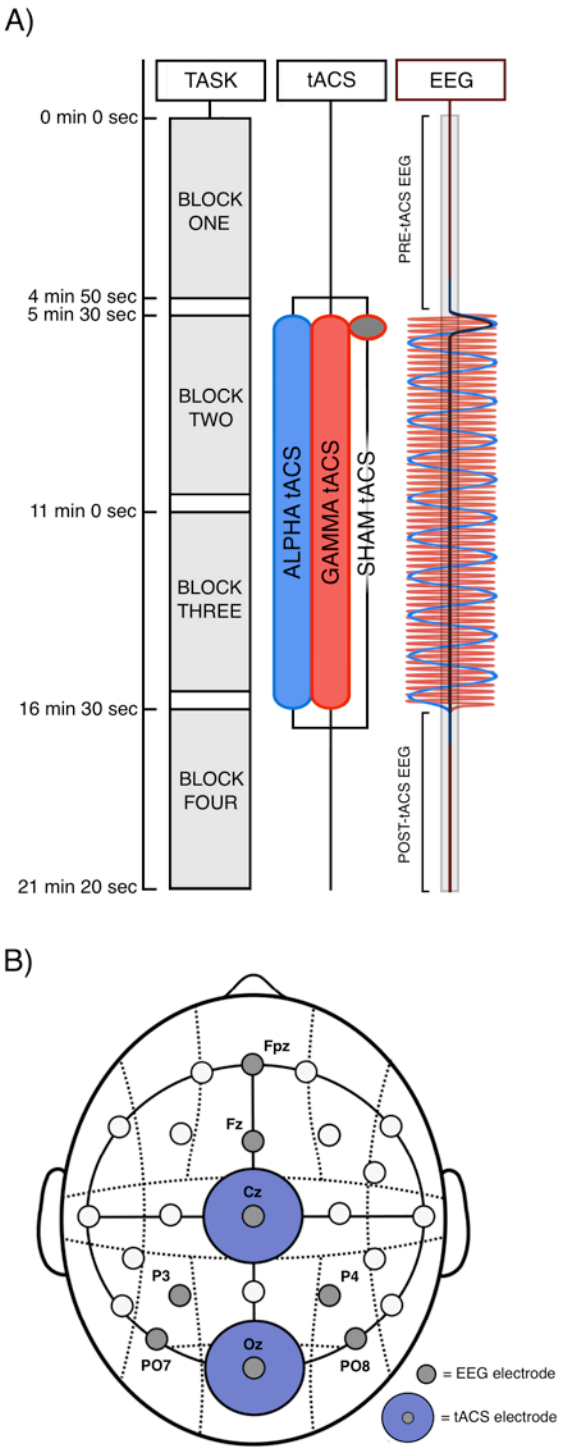


Figure 2

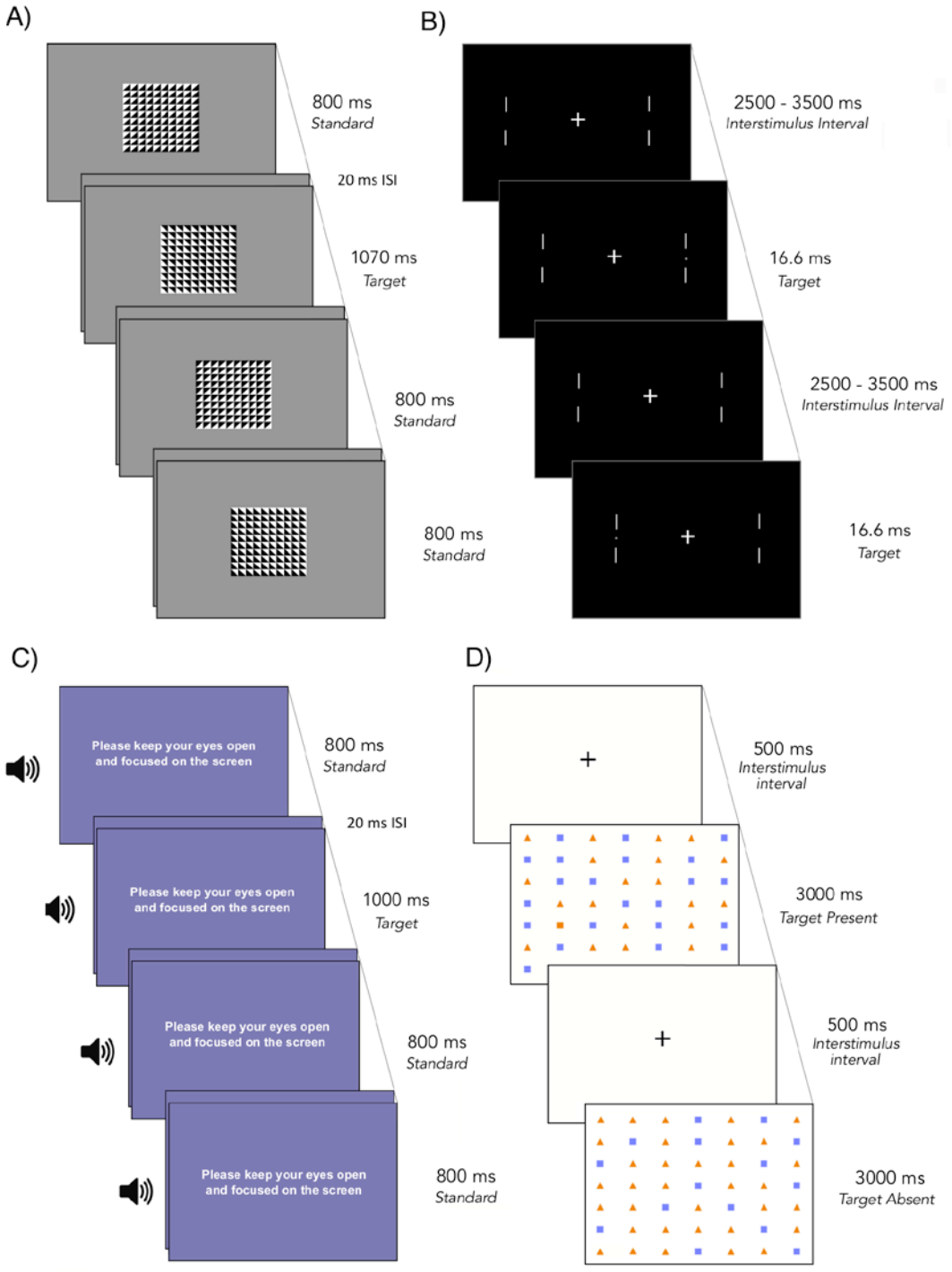

A)
800 ms
Standard
20 ms ISI
1070 ms
Target
800 ms
Standard
800 ms
Standard
B)
2500 - 3500 ms
Interstimulus Interval
16.6 ms
Target
2500 - 3500 ms
Interstimulus Interval
16.6 ms
Target
C)
Please keep your eyes open and focused on the screen
800 ms
Standard
20 ms ISI
Please keep your eyes open and focused on the screen
1000 ms
Target
Please keep your eyes open and focused on the screen
800 ms
Standard
Please keep your eyes open and focused on the screen
800 ms
Standard
D)
500 ms
Interstimulus interval
3000 ms
Target Present
500 ms
Interstimulus interval
3000 ms
Target Absent

Figure 3

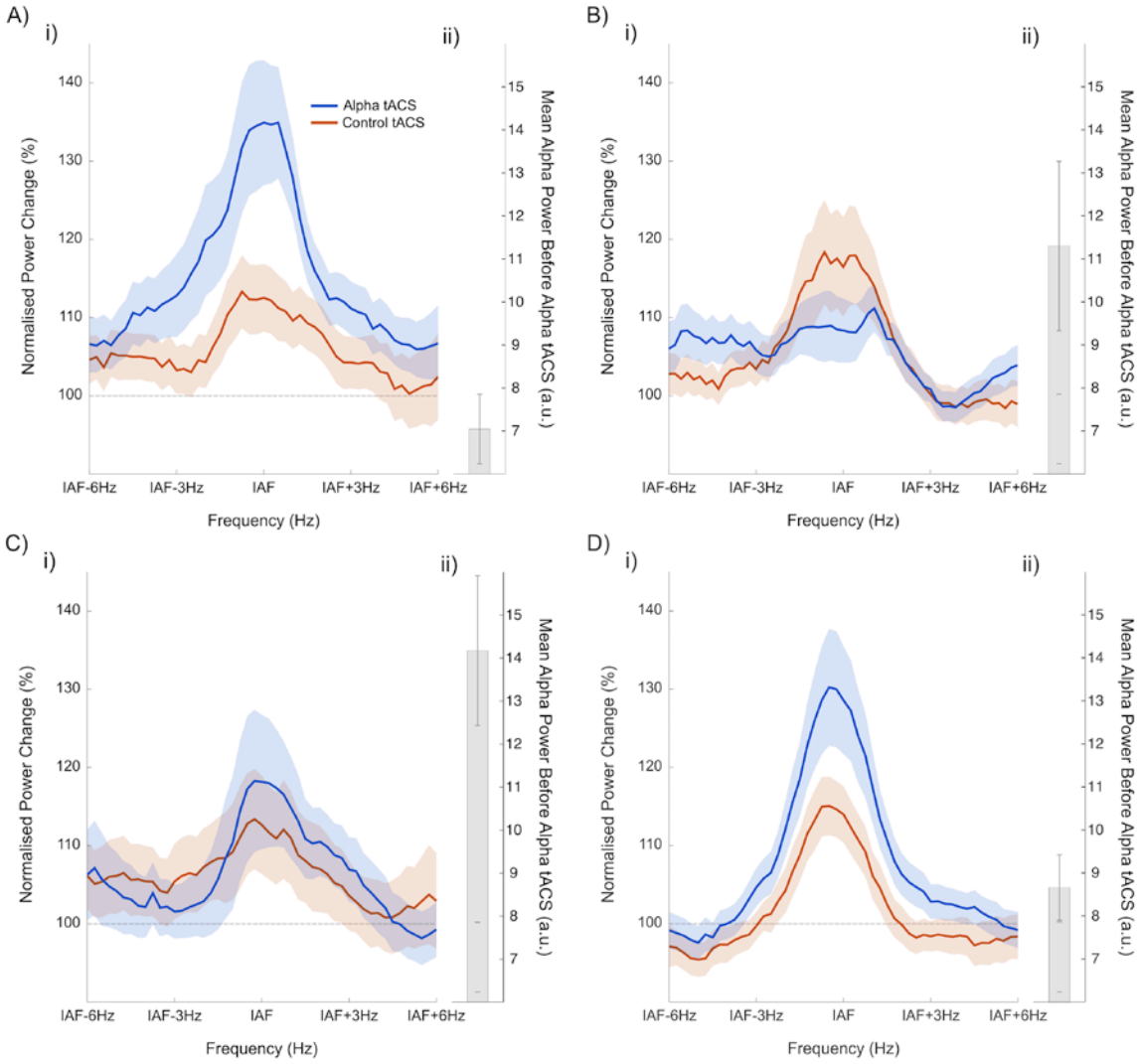

A)
i)
ii)
Alpha tACS
Control tACS
Normalised Power Change (%)
Mean Alpha Power Before Alpha tACS (a.u.)
IAF-6Hz
IAF-3Hz
IAF
IAF+3Hz
IAF+6Hz
Frequency (Hz)
B)
C)
D)

Figure 4

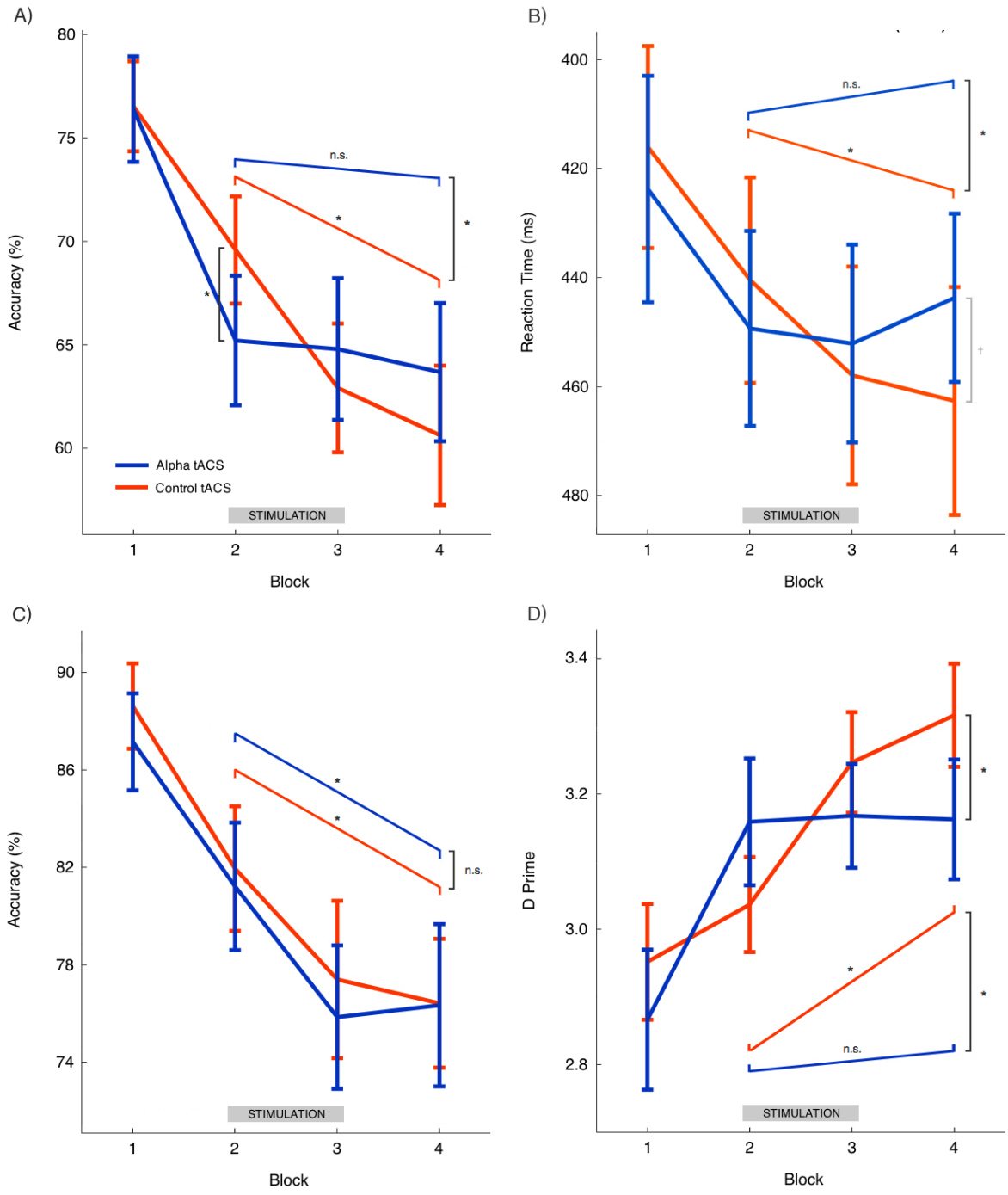

A)
Accuracy (%)
80
75
70
65
60
n.s.
*
*
*
Alpha tACS
Control tACS
STIMULATION
1
2
3
4
Block
B)
Reaction Time (ms)
400
420
440
460
480
n.s.
*
*
†
STIMULATION
Block
C)
Accuracy (%)
90
86
82
78
74
*
*
n.s.
STIMULATION
Block
D)
D Prime
3.4
3.2
3.0
2.8
*
*
n.s.
*
STIMULATION
Block

FIGURE LEGENDS

Figure 1 – Experimental Design.

A) *Experimental Session Design*. In all experiments, participants performed four task blocks, each lasting 4 minutes and 50 seconds. A fixed-duration break of 40 seconds was allowed between blocks. EEG was recorded before and after the delivery of stimulation. During alpha- and gamma-tACS, stimulation was applied for 11 minutes from the start of the second block to the start of the fourth block. During sham-tACS, stimulation was applied at 10 Hz during only the first 50 seconds of this period (including ramp-up and down times). In all experiments, participants performed two task sessions, separated by a break of 25 minutes. B) *Electrode placements*. EEG electrodes were positioned at PO7, PO8, P3, P4, Fz, and Fpz. tACS electrodes were positioned at Oz and Cz.

Figure 2 – Task designs.

A) *Visual Continuous Temporal Expectancy Task (Experiment 1).* Participants monitored a continuous stream of centrally presented, patterned stimuli. Standard stimuli (~91% of trials) were presented for 800 ms. Target stimuli (~9% of trials) were presented for a longer duration of 1070 ms. All stimuli were preceded by a 20 ms grey-screen interval. Participants were required to press the space bar following all target trials (O'Connell et al., 2009). B) *Visual Threshold Detection Task (Experiment 2).* A fixation cross, surrounded by two pairs of placeholders, was constantly present in the centre of the screen. With a variable inter-stimulus interval (2500-3500 ms), a grey dot was presented in the middle of either the left- or right-hand placeholders. These grey dots varied in their intensities. Participants were required to respond to the presentation of each dot by pressing the space bar as quickly as possible (Chaumon & Busch, 2014). *C) Auditory Continuous Temporal Expectancy Task*

(Experiment 3). Participants were repeatedly played an auditory stimulus. On standard trials (~91% of trials), this stimulus lasted 800 ms. On target trials (~9% of trials), this stimulus lasted 1000 ms. All stimuli were preceded by a 20 ms period of silence. As in the vCTET, participants were required to press the space bar following all target trials (Berry, Li, Lin, & Lustig, 2014). D) *Visual Conjunction Search Task (Experiment 4).* Participants were repeatedly presented with a 7 x 7 grid of coloured shapes (blue squares, orange triangles, and orange squares). Each grid was presented for 3000 ms, with a fixed inter-stimulus interval of 500 ms. If an orange square was present in a grid (50% of trials), participants were required to press 'M' as quickly as possible. If an orange square was not present (50% of trials), participants were required to press 'Z' (Gonzalez-Rosa et al., 2015).

Figure 3 – The effects of alpha- vs. control-tACS (sham- & gamma-tACS) on normalised change in EEG power across 4 experiments (centred around individual alpha frequency).

EEG data were recorded during blocks 1 and 4 in each experiment (i.e. before and after tACS). Individualised alpha bands were defined as 3 Hz above and below individualised alpha frequency (IAF). The effect of tACS on alpha power was then assessed by dividing post- by pre-stimulation EEG power (i.e. yielding a measure of normalised power change). A) *Visual Continuous Temporal Expectancy Task (Experiment 1)*, B) *Visual Threshold Detection Task (Experiment 2)*, C) *Auditory Continuous Temporal Expectancy Task (Experiment 3)*, D) *Visual Conjunction Search Task (Experiment 4)*. Coloured shading shows ±1 standard error of the mean. * = $p < .05$. IAF = Individual Alpha Frequency.

Figure 4 – The effects of alpha- vs. control-tACS (sham- & gamma-tACS) on sustained attention task performance across 4 experiments.

Participants performed 4 blocks of four different tasks (each block lasting 4 minutes and 50 seconds). A) *Visual Continuous Temporal Expectancy Task (Experiment 1)*, B) *Visual Threshold Detection Task (Experiment 2)*, C) *Auditory Continuous Temporal Expectancy Task (Experiment 3)*, D) *Visual Conjunction Search Task (Experiment 4)*. In all experiments, tACS was delivered from the start of block 2 to the start of block 4. Note that the y-axis in B) has been flipped to aid comparability with Experiment 1. Error bars show ±1 standard error of the mean. * = $p < .05$.

Supplementary Figure 1 – The effects of alpha- vs. control-tACS on normalised change in EEG power (centred around individual alpha frequency), broken down by experimental group.

Data are presented from Experiment 1 in the top-left panel, from Experiment 2 in the top-right panel, from Experiment 3 in the bottom-left panel, and from Experiment 4 in the bottom-right panel. Within each panel, data from all participants are shown in the far left figure (I). To the right of this figure, data for participants receiving sham- (II) and gamma-tACS (III) are shown in the upper row (left vs. right), while data for participants receiving alpha-tACS in the first (IV) and second task sessions (V) are shown in the lower row (left vs. right). Coloured shading shows ±1 standard error of the mean.

Supplementary Figure 2 – Percentage accuracy and reaction times for Experiments 1 & 2, broken down by experimental group.

Percentage accuracy results are plotted in all left panels, while reaction times are plotted in all right panels. Results from Experiment 1

shown at the top, while results from Experiment 2 are shown at the bottom. For each experiment and behavioural measure, data from all participants are shown in the far left figure (I). To the right of this figure, data for participants receiving sham- (II) and gamma-tACS (III) are shown in the upper row (left vs. right), while data for participants receiving alpha-tACS in the first (IV) and second task sessions (V) are shown in the lower row (left vs. right). Error bars show ±1 standard error of the mean.

Supplementary Figure 3 – Percentage accuracy / D' and reaction times for Experiments 3 & 4, broken down by experimental group.

Data are plotted in an identical manner to Supplementary Figure 2. Results from Experiment 3 shown at the top, while results from Experiment 4 are shown at the bottom.

Supplementary Figure 4 – Event-related potential (ERP) data for all experiments.

Mean ERPs are plotted for EEG recorded before and after the delivery of alpha- vs. control-tACS in all experiments. For each experiment, ERPs were averaged from electrodes PO7, PO8, P3, and P4 from -200 ms before to 800 ms after the onset of task stimuli. These ERPs were then baseline corrected by subtracting from each ERP its mean amplitude from -200 to 0 ms. For Experiments 1, 3, and 4, ERPs are shown in response to all stimulus presentations. For Experiment 2, ERPs are shown only for stimuli that were correctly detected by participants. However, ERPs following all

stimulus presentations in Experiment 2 also show no differences between alpha- and control-tACS. For all experiments, ERPs before and after alpha-tACS are presented in the top panel, ERPs before and after control-tACS are presented in the middle panel, and ERPs after minus before alpha- vs. control-tACS are presented in the bottom panel.