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Opposite effects of lateralised transcranial alpha versus gamma stimulation on auditory spatial attention

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ABSTRACT

Background: Spatial attention relatively increases the power of neural 10-Hz alpha oscillations in the hemisphere ipsilateral to attention, and decreases alpha power in the contralateral hemisphere. For gamma oscillations (>40 Hz), the opposite effect has been observed. The functional roles of lateralised oscillations for attention are currently unclear.
Hypothesis: If lateralised oscillations are functionally relevant for attention, transcranial stimulation of alpha versus gamma oscillations in one hemisphere should differentially modulate the accuracy of spatial attention to the ipsi-versus contralateral side.
Methods: 20 human participants performed a dichotic listening task under continuous transcranial alternating current stimulation (tACS, vs sham) at alpha (10 Hz) or gamma (47 Hz) frequency. On each trial, participants attended to four spoken numbers on the left or right ear, while ignoring numbers on the other ear. In order to stimulate a left temporo-parietal cortex region, which is known to show marked modulations of alpha power during auditory spatial attention, tACS (1 mA peak-to-peak amplitude) was applied at electrode positions TP7 and FC5 over the left hemisphere.
Results: As predicted, unihemispheric alpha-tACS relatively decreased the recall of targets contralateral to stimulation, but increased recall of ipsilateral targets. Importantly, this spatial pattern of results was reversed for gamma-tACS.
Conclusions: Results provide a proof of concept that transcranially stimulated oscillations can enhance spatial attention and facilitate attentional selection of speech. Furthermore, opposite effects of alpha versus gamma stimulation support the view that states of high alpha are incommensurate with active neural processing as reflected by states of high gamma.

Introduction

When humans focus their attention to one location in space, neural oscillatory alpha power (~10 Hz) relatively increases in sensory areas in the hemisphere ipsilateral to attention and decreases in the contralateral hemisphere [1–3]. The prevailing functional interpretation is that high ipsilateral alpha power inhibits cortical activity in the hemisphere processing the unattended side of space, which agrees with the functional inhibition theory of alpha oscillations [4,5]. This view receives further support by studies showing that gamma power (>40 Hz), which reflects active cortical processing [6] and correlates negatively with alpha power [7], lateralises in the opposite way compared to alpha power during spatial attention [8–10]. In the present combined behavioural and tACS (transcranial alternating current stimulation) study, we test whether lateralised alpha and gamma oscillations, when externally stimulated, modulate accuracy of auditory spatial attention.

In the visual modality, rhythmic unihemispheric transcranial magnetic stimulation (rTMS) at alpha frequency has been shown to enhance perception [11] and to improve memory for targets ipsilateral to stimulation [12]; for a review, see Ref. [13]. In audition, however, the existence of an auditory alpha rhythm [14] and functional roles thereof are notoriously more challenging to assess experimentally [15,16]. Also, the link between auditory alpha oscillations and spatial attention is purely correlational so far: In a recent magnetoecephalograhphy (MEG) study using a dichotic listening task [17], we found stronger alpha lateralisation (i.e., high

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ipsi- and low contralateral alpha power) in correct versus incorrect trials (Fig. 1A&C).

Although transcranial electric stimulation (tES) at standard stimulation intensities (i.e., <4 milliamps) is arguably too weak to trigger neural firing [18], intracranial and subcortical recordings show that tES modulates the excitation level of stimulated areas [19,20]. In particular, tACS entrains neural oscillations at the stimulated frequency and increases the amplitude of stimulated alpha or gamma oscillations [21–24]. Since tES affects currently engaged neural structures most strongly [25,26], we used a unihemispheric tACS setup in order to target a superior temporal/inferior parietal cortex region in the left hemisphere (Fig. 1D), which was found before to exhibit marked and directly performance-related alpha lateralisation during auditory spatial attention [17].

If lateralised oscillatory power were a mere corollary of neural processes that do instantiate attention, alpha- and gamma-tACS should not affect accuracy of spatial attention. However, our findings demonstrate that left hemispheric alpha-versus gamma-tACS do modulate oppositely the recall of attended speech on the left versus right side. This suggests that lateralised oscillations are a functionally significant substrate of spatial attention.

Materials and methods

Participants

Twenty young healthy participants (19–31 years, 10 females) with no history of neurological or psychiatric disorders participated. One of the participants was not fully right-handed (laterality quotient of 20 on a scale from −100 [left-handed] to +100 [right-handed]) according to the Edinburgh inventory [27]. Two participants were non-German native speakers but of sufficient German language proficiency to perform the task. Experimental procedures were approved by the local ethics committee of the University of Oldenburg (Kommission für Forschungsfolgenabschätzung und Ethik).

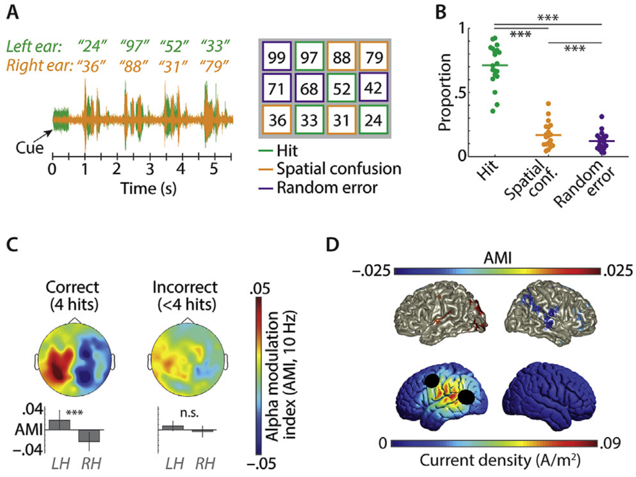

Fig. 1. (A) Dichotic listening task. A cue tone on one ear (left in this example) indicated the to-be-attended side. Four spoken numbers were presented to the left ear, and four different (same-talker) numbers to the right ear. The task was to select the four to-be-attended target numbers from a visually presented number pad shown after auditory stimulation. Colored edges (not shown during the experiment) illustrate different response types. (B) Colored dots and horizontal lines show respective individual ($n = 20$) and average proportions (across all experimental conditions and sessions) of different response types. For data of individual conditions, see Supplementary Materials (Fig. S1). (C) Topographies show the alpha modulation index (AMI) obtained in a previous magnetoencephalography (MEG) study using the same task [17] by contrasting attend-left versus attend-right trials: (attend-left−attend-right)/(attend-left + attend-right), in the time interval from cue onset to first number onset (where the strongest lateralisation was observed) for correct trials (left; 4 hits; significant difference in AMI for left (LH) versus right-hemisphere (RH) sensors; $^{***}p < 0.001$) and for trials containing incorrect responses (right; <4 hits; n.s. $p > 0.05$). (D, top) Source localization of the AMI (for all trials and the entire trial duration) in Ref. [17] revealed strong engagement of bilateral superior temporal/inferior parietal cortex regions in the modulation of alpha power during spatial attention. Overlays on brain surfaces are masked for $p < 0.05$; uncorrected. (D, bottom) Stimulation (at electrode positions TP7 and FC5; black dots) was intended to target task-engaged regions in the left but not in the right hemisphere. Simulation of current densities calculated in SimNIBS [69].

Auditory stimuli

We used German, 4-syllable numbers, spoken by a trained female voice, from previous studies [28,29]. Recordings of spoken numbers from 21 to 99 (excluding integer multiples of 10) with a sampling rate of 44.1 kHz were shortened in Praat (version 6.0.14) by a factor of 0.85, resulting in a mean (±SD) number duration of 0.96 s (±0.05). We determined the perceptual center (P-center) of each number [30] as the time point when the number signal's broad-band envelope (15-Hz lowpass-filtered modulus of the Hilbert transform) reached 50% of the first syllable's peak. In the following, the onset of a number refers to its perceptual center. The spatial cue was a monaural 1000-Hz sine tone of 500-ms duration.

Dichotic listening task

The dichotic listening task was a slightly speeded version of a task used previously [17]. For each trial, eight different numbers were selected randomly from the pool of all numbers; four to-be-presented to the left, the other four to-be-presented simultaneously to the right ear. For simultaneously presented numbers on the left and right ear, perceptual centers were temporally aligned and numbers were distinct in their first and second digit (e.g., co-occurences of "35" and "37" or "81" and "21" were avoided).

Each trial started with the presentation of the cue (to one ear) to indicate whether participants had to attend to the left or right. The cue was followed (after 500 ms) by four spoken numbers presented to the left ear and simultaneously by four different numbers presented to the right ear (Fig. 1A). The onset-to-onset time interval of two subsequent numbers was 1.25 s. Presentation of acoustic stimuli (cue and numbers) took on average (±SD) 5.66 s (±0.04). Cue tone and spoken numbers were embedded in continuous white background noise (+10 dB SNR). Cue tone and background noise had 50-ms linear onset and offset ramps.

Approximately 0.5 s (jittered 0.3–0.7 s) after the offset of the last two simultaneous numbers a response screen was shown that contained 12 numbers (four from the to-be-attended side, four from the to-be-ignored side, and four random numbers not presented on any side). Participants were asked to use a mouse to select the four numbers that appeared on the to-be-attended side in any order. Numbers on the response screen were presented in either ascending or descending order (randomised from trial to trial) to prevent motor preparation during a trial. After selection of four numbers, the next trial started automatically (after approximately 1 s, randomly jittered 0.8–1.2 s). Auditory materials were presented via Sennheiser HD 25–1 II headphones. In one run of the experiment a participant performed 110 trials, which took on average 26'31'' (±2'4'' SD) to complete. Trial order was fully randomised with the constraint that the spatial cue appeared on the left side in half of the trials in each run.

tACS stimulation

We used an unihemispheric tACS stimulation setup, which was designed to target left-hemispheric posterior superior temporal gyrus (pSTG) and surrounding auditory and parietal cortex regions.

In an experiment on auditory gap detection a combarable tACS setup was shown to successfully modulate auditory processing [31]. We stimulated the left (instead of the right) hemisphere since we had previously found that the modulation of oscillatory power by spatial attention in the left (versus the right) hemisphere was more specific to the alpha frequency of 10 Hz [17].

Round electrodes of 3 cm diameter were placed on the scalp at sites FC5 and TP7 according to the international 10-10 system (Fig. 1D). Electrodes were attached to the respective positions using Ten20 conductive paste (Weaver and company, Aurora, USA) and impedance was kept below 10 kΩ. The stimulator (DC stimulator plus, Eldith, 419 NeuroConn, Ilmenau, Germany) emitted a sinusoidal alternating current with no DC offset at frequencies of either 10 Hz (alpha) or 47.1 Hz (gamma) at a strength of 1 mA (milliampere) peak-to-peak. The gamma stimulation frequency of 47.1 Hz was chosen to not match a multiple of the alpha frequency. Stimulation amplitude was ramped up and down linearly over 20 or 94.2 cycles (2 s) for 10 Hz and 47.1 Hz stimulation frequencies, respectively. tACS was applied continuously for 25 min between the two ramping periods.

A simulation of the current density on the cortical surface indicates that our stimulation setup is suitable to stimulate the desired left hemispheric target region while leaving right hemispheric areas unmodulated (Fig. 1D). For sham stimulation, the tACS setup was the same, except that the stimulation consisted only of the ramping periods at the beginning and subsequently remained off for the rest of the run.

Procedure

In total, each participant performed four runs of the dichotic listening task (resulting in 4 × 110 = 440 trials), separated in two sessions taking place on different days: alpha session (sham run & alpha-tACS run) and gamma session (sham run & gamma-tACS run). Session order (alpha–then–gamma vs gamma–then–alpha) was balanced across participants and the two sessions were separated by 5–14 days (M = 7.58 days).

Each session started with a short training to familiarise the participant with the task procedure. Next, participants performed the sham run, followed by a short break and the alpha/gamma-tACS stimulation run (Fig. 2A). Since recall of auditory stimuli on the left versus right side in dichotic listening tasks is known to be of limited test–retest reliability in the individual [32,33], we included a sham run immediately before the tACS run in each experimental session. tACS effects could be quantified by contrasting each participants' tACS run with the sham run of the respective session.

Within each session the sham run was tested first in order to avoid possible confounds of tACS after-effects, which are known to outlast the duration of stimulation considerably [34,35]. Note, however, that possibly enhanced/reduced performance in the later tACS run compared to the earlier sham run is orthogonal to our frequency- and spatially-specific hypotheses (Fig. 2B).

Statistical analyses

The major dependent measure in the present study was the proportion of correctly recalled numbers (i.e., proportion hits). On each trial participants selected four numbers from the response screen, resulting in five possible proportions of correctly recalled numbers: 4/4, 3/4, 2/4, 1/4, or 0/4.

The study implemented a 2 (session: alpha vs gamma) × 2 (stimulation: sham vs tACS) × 2 (to-be-attended side: left vs right) within-subject design. For the statistical analysis of tACS effects, we fitted linear mixed-effects models using the *lme4* package for R (version 2017-03-06) and Rstudio (version 1.0.136). In essence, participants' single-trial data were used to model the response variable proportion correct on the three predictors. Additional statistical control analyses, which control for potentially confounding variables (session order, handedness, single-trial onset time), are described in the Supplemental Materials. To obtain *p*-

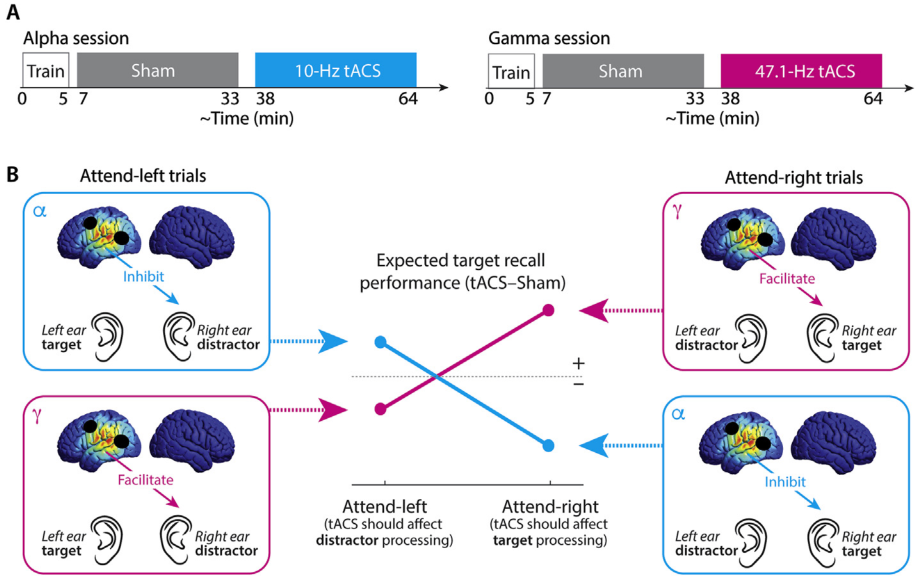

Fig. 2. (A) The experiment was divided in two sessions (counterbalanced session order across participants), which took part on different days. In each session, participants first performed a short training, followed by a sham run of the experiment without tACS stimulation, a short break, and another run of the experiment under continuous tACS stimulation lasting 25 min (alpha session: 10 Hz; gamma session: 47.1 Hz). (B) Expected effects of left-hemispheric tACS stimulation on auditory spatial attention. Alpha-tACS (α; blue boxes and blue lines) was expected to increase the inhibition of the contralateral right-ear input. If the distractor is inhibited (in attend-left trials; top left box) recall of targets should increase compared to sham; if the target is inhibited (in attend-right trials; bottom right box) recall of targets should decrease. Gamma-tACS (γ; pink boxes and pink lines) was expected to facilitate processing of the of contralateral right-ear input, which should accordingly reverse the effect of alpha-tACS. The effect of tACS was expected to be larger in attend-right trials, since only here our left-hemispheric tACS stimulation should directly affect processing of the target stimulus (opposed to attend-left trials, where left-hemispheric tACS affects distractor processing). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

values for predictors [36], we used the *anova* function using Satterthwaite approximation implemented in the *lmerTest* package. These *p*-values were compared to *p*-values obtained with the *mixed* function using parametric bootstrapping implemented in the *afex* package, which yielded almost identical results.

For visualization of tACS effects (Fig. 3), we logit-transformed the proportion correct data for each subject and condition [37], followed by calculation of the tACS effect (tACS−sham), separately for the alpha and gamma session.

Side effects of tACS

According to questionnaires [38] answered in the end of each session (alpha & gamma), the side effects reported by most of our 20 participants were tingling (alpha: 18; gamma: 15), difficulty in concentration (alpha: 17; gamma: 15), and tiredness (alpha: 12; gamma: 10). However, only a subset of participants attributed these side effects to the tACS stimulation (tingling, alpha: 13, gamma: 12; difficulty in concentration, alpha: 7, gamma: 6; tiredness, alpha: 5, gamma: 4). Intensities of these side effects (rated on a scale from 0 = 'no' to 4 = 'strong') did not differ between alpha and gamma sessions (Wilcoxon signed rank tests; all $p > 0.1$).

Participants were also asked in the end of each session to indicate for individual runs of a session (sham & tACS) whether they think they were stimulated. For the alpha session, 7 participants reported stimulation during sham and 12 during tACS (McNemar test; $p = 0.18$). For the gamma session, 6 participants reported stimulation during sham and 15 during tACS ($p = 0.012$). Stronger sensation of stimulation in the gamma session might explain a change in overall performance but not our specific hypothesised response patterns (i.e., differential performance modulation in attend-left versus attend-right trials; see Fig. 2B). We thus consider these side effects uncritical to the results of the present study.

Effect sizes

Since there are no standard effect size measures for individual predictors and their interactions in linear mixed models, we report the unstandardized coefficient (*b*), which corresponds to the estimated change in the dependent variable (proportion correctly recalled numbers) when the predictor increases by one level. For repeated-measures ANOVAs, we report partial eta squared (η^2_P). For t-tests, we report r-equivalent (bound between 0 and 1; [39]).

Results and discussion

In humans, left auditory cortex regions receive input predominantly from the right ear and vice versa for right auditory cortex [40,41]. Therefore, our tACS setup, which targeted left auditory and parietal regions, was expected to affect neural processing of the right-ear input in a highly predictable way (Fig. 2B): Left-hemispheric alpha-tACS should inhibit neural processing of the right-ear input, leading to reduced accuracy in attend-right trials but enhanced accuracy in attend-left trials compared to sham. Contrary, left-hemispheric gamma-tACS should facilitate neural processing of the right-ear input, leading to enhanced accuracy in attend-right trials but reduced accuracy in attend-left trials.

Confusion of attended and ignored speech

Across all experimental sessions (alpha/gamma-tACS, sham) and conditions (attend-left/right), proportions of hits, spatial confusions and random errors differed significantly (Fig. 1B; repeated-measures ANOVA; $F_{2,\,38} = 108.8$; $p < 0.001$; $\eta^2_P = 0.851$). Replicating results of previous studies using the same task [17,42], the proportion of hits was higher than spatial confusions ($t_{19} = 9.51$; $p < 0.001$; $r = 0.91$) and random errors ($t_{19} = 11.73$; $p < 0.001$; $r = 0.94$). Critically, the proportion of spatial confusions was higher than random errors ($t_{19} = 3.99$; $p < 0.001$; $r = 0.68$), which indicates significant interference of distractors with to-be-attended target speech (proportions of response types for individual experimental sessions and conditions are shown in the Supplementary Materials, Fig. S1).

Alpha- and gamma-tACS differentially modulate auditory spatial attention

Most importantly, and directly in line with our hypotheses, the session × stimulation × to-be-attended side interaction was significant (Fig. 3; $b = 0.062$; $F_{1,\ 8773} = 11.68$; $p < 0.001$). In detail, alpha-tACS compared to sham (blue line in Fig. 3A) enhanced the

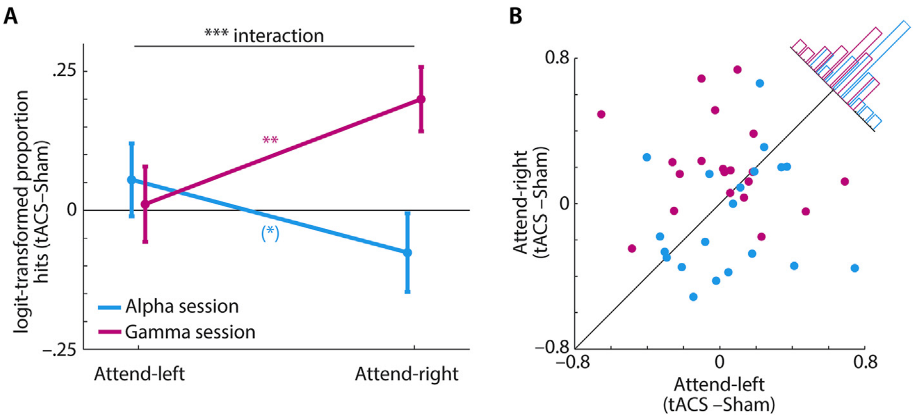

Fig. 3. (A) Opposite effects of alpha-versus gamma-tACS on spatial attention. For visualization, effects of tACS were quantified by contrasting each participant's logit-transformed proportion of correct responses (hits) in the tACS run with the sham run of the respective session. Alpha-tACS compared to sham enhanced performance in attend-left versus attend-right trials ((*) $p = 0.059$), while gamma-tACS compared to sham enhanced performance in attend-right versus attend-left trials (**$p = 0.003$). The interactive effect of alpha-versus gamma-tACS (compared to sham) on performance in attend-left versus attend-right trials was highly significant (***$p < 0.001$). (B) 45-degree plot shows logit-transformed proportion correct data for attend-left (x-axis) versus attend-right trials (y-axis) for individual (n = 20) participants. The corner histogram highlights that alpha-tACS relatively enhanced performance in attend-left trials (blue dots tend to be below the diagonal), whereas gamma-tACS relatively enhanced performance in attend-right trials (pink dots tend to be above the diagonal). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

proportion correct in attend-left trials but decreased the proportion correct in attend-right trials (stimulation × to-be-attended side interaction: $b = -0.024$; $F_{1,\ 4377} = 3.57$; $p = 0.059$). For gamma-tACS compared to sham (pink line in Fig. 3B) the pattern of results precisely reversed (stimulation × to-be-attended side interaction: $b = 0.038$; $F_{1,\ 4377} = 8.83$; $p = 0.003$). These findings remained significant when we controlled for session order, handedness, and single-trial onset time (see Supplemental Materials).

It is of note that the effect of tACS-induced performance modulation shown in Fig. 3 is of considerable size: Alpha-versus gamma-tACS compared to sham modulated performance by ~1.1% in attend-left trials, but by ~5.1% in attend-right trials. Given an average accuracy of 71.15%, this amounts to an average-corrected relative performance modulation of ~1.5% in attend-left trials and ~7.2% in attend-right trials by tACS; for a similar method to compute relative performance modulation, see Ref. [43].

So far, electric-stimulation studies targeting one hemisphere have found shifts of visuo-spatial attention in case of transcranial direct current stimulation (tDCS; [44–47]), whereas tACS at alpha frequency has produced inconclusive [48] or non-replicable results [49]. One previous study aimed at modulating auditory spatial processing using tDCS applied to either the left or right hemisphere during dichotic listening but did not observe hemisphere-specific performance modulations [50]. To the contrary, the opposing effects of left-hemispheric alpha-versus gamma-tACS observed in the present study show that transcranially stimulated lateralised oscillations modulate the focus of auditory attention in a frequency-specific way: tACS-stimulation of alpha oscillations inhibits the attentional selection of speech presented contralateral to the stimulated hemisphere, while tACS-stimulation of gamma oscillations facilitates it. Both, lateralised alpha and gamma oscillations, thus bear functional relevance in auditory spatial attention.

There is good reason to assume that our fixed stimulation frequencies of 10 Hz and 47.1 Hz were close in frequency to intrinsic neural oscillatory responses, which is critical in order to effectively entrain neural oscillatory activity [51]. First, peak frequencies of respective alpha and gamma power lateralisation during spatial attention are typically close to 10 Hz [1,17,52] and 40–80 Hz [8]. Second, electrocorticography recordings from auditory cortex regions, which were among the stimulated regions in the present study, have shown that attending versus ignoring auditory stimuli induces narrow-band alpha power modulation centered around 10 Hz [53], and that the auditory-induced gamma synchronisation is rather broad in frequency [40–120 Hz]; [54], including our stimulation frequency of 47.1 Hz.

Our participants were stimulated continuously for 25 min and, since the trial timing was not fixed but depended on a participant's response speed, the onsets of auditory events (cue tone and numbers) were randomly distributed across the cycle of the stimulated alpha or gamma oscillation. Thus, whereas previous research found phase effects of alpha-tACS on auditory perception [55], the present study demonstrates that tACS modulates spatial attention to auditory events which are non-phase-locked to the stimulated oscillation.

Based on the theoretically proposed [4] and empirically observed opposing roles of inhibitory alpha and facilitatory gamma power for spatial attention [56], we expected unihemispheric gamma-tACS to reverse the effect of alpha-tACS. Our results confirm this. Previous tACS studies have shown that high-frequency random-noise stimulation (100–640 Hz) targeting auditory cortex enhanced auditory responses in the EEG [57] and improved auditory gap-detection performance [58]. Together with these studies, our results support the view that gamma-tACS has the potency to increase sensitivity to auditory stimuli and to facilitate auditory processing, which thus affects auditory spatial attention inversely compared to tACS-entrained inhibitory alpha oscillations.

Left-hemispheric tACS predominantly affects attend-right trials

Separate analyses of attend-left and attend-right trials revealed that the session (alpha vs gamma) × stimulation (tACS vs sham) interaction was significant for attend-right trials ($b = 0.051$; $F_{1,\ 4377} = 17.41$; $p < 0.001$) but not for attend-left trials ($b = -0.011$; $F_{1,\ 4377} = 0.67$; $p = 0.413$). We assume that this is due to our left-hemispheric locus of stimulation, which, due to the contralateral organization of the human auditory system, modulated auditory processing of task-relevant target speech predominantly in attend-right trials but processing of task-irrelevant distractor speech in attend-left trials (see Fig. 2B). Recall accuracy in the dichotic listening task likely depends more on attending to target speech, and hinges only indirectly on ignoring the distractor; for a similar argument, see Ref. [59]. These results thus suggest that the impact of tACS-stimulated oscillations of either frequency on target speech (in attend-right trials) was larger than the impact of tACS-stimulated oscillations on distractor speech (in attend-left trials).

Note that stronger effects of left-hemispheric alpha- and gamma-tACS in attend-right trials indirectly support the feasibility of our stimulation setup in targeting primarily regions in the left hemisphere (Fig. 2B). In theory, right- instead of left-hemispheric tACS in our dichotic listening task should induce stronger performance modulations in attend-left trials. However, functional asymmetries of left versus right auditory cortex regions could further complicate this reasoning [60,61]. In particular, despite the observed symmetry of lateralised alpha oscillations across the two hemispheres during spatial attention to speech [3,17,42], it is important to note that we stimulated only the left hemisphere in the present study, which responds to speech stimuli predominantly (for reviews, see Refs. [62,63]) and exhibits oscillatory top-down signals during speech processing [64]. Thus, it is conceivable that stimulation of the left hemisphere is particularly effective when the spatial attention task at hand requires processing of speech materials.

Functional roles of lateralised alpha and gamma oscillations

Strikingly, the pattern of our results is in accordance with the hypothesised roles of lateralised inhibitory alpha and facilitatory gamma oscillations for spatial attention (Fig. 2B). It is important to note, however, that even experiments employing perturbation techniques such as tACS allow only limited causal inference [65]. For instance, it might be that tACS-stimulated lateralised alpha oscillations causally inhibit neural processing in the stimulated brain regions, whereas tACS-stimulated gamma oscillations are causally ineffective by themselves but instead provide a means to decrease the power of causally effective alpha oscillations; for an effect of gamma-tACS on alpha oscillations, see Ref. [66].

Furthermore, our results do not reveal at which level of neural processing tACS-stimulated alpha and gamma oscillations are effective. First, our participants were stimulated continuously for 25 min while they performed the dichotic listening task, which complicates inference regarding the particular time interval in which the tACS-stimulated alpha and gamma oscillations affected task performance. Given that the strongest lateralisation of alpha oscillations occurs during anticipation and processing of speech stimuli in the present task design [17,42], it is most likely that stimulation of lateralised oscillations by alpha- and gamma-tACS affected task performance during these time intervals.

Second, since our tACS-stimulation targeted the junction of superior temporal and inferior parietal cortical regions, we cannot isolate contributions of lateralised oscillations in auditory sensory areas versus supramodal attention areas here. In fact, both neurostimulation of spatial auditory processing but also of spatial attention would eventually affect the recall of numbers on the side ipsi- vs contralateral to stimulation in the present design. In line with the predominant views on the functional roles of neural oscillations (e.g., Ref. [67]), it is reasonable to assume that alpha-tACS affects behaviour through inhibition of (top-down) attention to one side of space whereas gamma-tACS affects behaviour through facilitation of neural (bottom-up) encoding (see e.g., Ref. [10]) of auditory stimuli in left versus right auditory cortex. Alternatively, alpha- and gamma-tACS might affect the same neural processes but in opposite direction, but this view is somewhat weakened by the present data: the effects of alpha- and gamma-tACS on the recall of target numbers (i.e., tACS–sham, logit transformed) were not significantly negatively correlated (attend-left trials: $r = 0.19$; $p = 0.427$; attend-right trials: $r = 0.02$; $p = 0.938$). Combining region-specific brain stimulation, neuroimaging, and behavioural measures should test these alternative explanations in future studies [68].

Conclusions

Lateralised neural oscillations across the cerebral hemispheres are a well-known signature of spatial attention. Here, we show that unihemispheric transcranial alternating current stimulation of alpha and gamma oscillations holds the power to modulate spatial attention to speech. In agreement with prevailing views on neural alpha and gamma oscillations, our results support the functional relevance of these regimes of neural oscillations for spatial attention in general: The attentional selection of speech presented to the left or right side is inhibited when alpha-tACS targets the contralateral hemisphere (and vice versa for gamma-tACS).

Declarations of interest

CSH has filed a patent application for brain stimulation and received honoraria as editor from Elsevier Publishers, Amsterdam.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.brs.2018.04.006.

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