

Causal links between parietal alpha activity and spatial auditory attention

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1 **Abstract**

2 Both visual and auditory spatial selective attention result in lateralized alpha (8-14 Hz) oscillatory
3 power in parietal cortex: alpha increases in the hemisphere ipsilateral to attentional focus. Brain
4 stimulation studies suggest a causal relationship between parietal alpha and suppression of the
5 representation of contralateral visual space. However, there is no evidence that parietal alpha
6 controls auditory spatial attention. Here, we performed high definition transcranial alternating
7 current stimulation (HD-tACS) on human subjects performing an auditory task in which they
8 attended either spatial or nonspatial features. Alpha (10 Hz) but not theta (6 Hz) HD-tACS of right
9 parietal cortex interfered with attending left but not right auditory space. Parietal stimulation had
10 no effect for nonspatial auditory attention. Moreover, performance in post-stimulation trials
11 returned rapidly to baseline. These results demonstrate a causal, frequency-, hemispheric-, and
12 task-specific effect of parietal alpha brain stimulation on top-down control of auditory spatial
13 attention.

14 **1. Introduction**

15 *1.1 Parietal alpha activity changes with the focus of spatial attention*

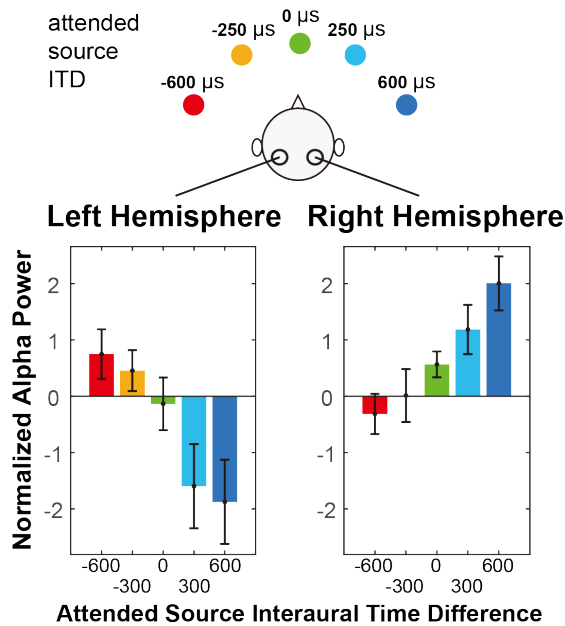
16 Parietal cortex interacts with frontal cortex to control spatial attention in both vision and
17 audition^{1,2}. Functional magnetic resonance imaging (fMRI) reveals a series of retinotopically
18 mapped regions ascending along the intraparietal sulcus (IPS), which are biased towards
19 representing contralateral exocentric space^{3,4}. While the earlier mapped regions are strongly
20 engaged only by vision, the higher maps are recruited when participants engage spatial auditory
21 attention⁵.

22 Alpha oscillations (8-14 Hz) are associated with a range of neural functions^{6,7}. Parietal cortex
23 generates strong alpha oscillations measurable using electro- and magneto-encephalography (EEG
24 and MEG)⁸⁻¹⁰. When listeners focus visual attention, alpha power lateralizes, increasing in the
25 parietal hemisphere ipsilateral to the direction of attention and decreasing contralaterally¹¹.
26 Auditory spatial attention also results in lateralized parietal alpha activity¹²⁻¹⁶; indeed, alpha
27 lateralization shifts systematically as the focus of auditory spatial attention shifts from far-left to
28 far-right^{13,17} (see Figure 1A). These results suggest that focusing spatial attention in both vision
29 and audition leads to similar parietal alpha activity.

30 While auditory spatial processing relies on retinotopic regions of parietal cortex, processing
31 nonspatial features does not, even when listeners are attending the same source in the same sound
32 mixture^{5,18,19}. Indeed, for a target defined by its location, alpha lateralization appears only
33 transiently at the start of a trial if competing streams have distinct nonspatial features²⁰. Thus,
34 spatial auditory attention utilizes parietal cortex and produces lateralized alpha; however,
35 nonspatial auditory attention does not and produces no signature of attentional focus in parietal
36 cortex.

A. Effect of direction of attention

(adapted from Deng et. al.)



B. Effect of talker discontinuity

(adapted from Mehraei et. al.)

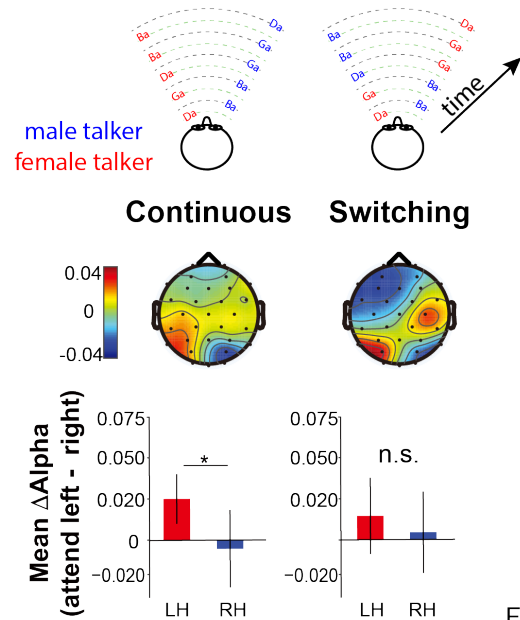


Figure 1

37

38 *Figure 1. Summary of previous results exploring lateralization of alpha power during auditory spatial*
 39 *attention processing. A) Adapted with permission from ¹⁷. Average normalized alpha activity (relative to*
 40 *global field power of alpha, calculated over N=26 subjects) in left and right parietal EEG sensors measured*
 41 *in an auditory spatial attention task. Spatial attention was covertly directed to one of five different lateral*
 42 *positions (see top of the panel), controlled by changing the interaural time difference (ITD) of the target*
 43 *stimulus. The average of alpha power during a preparatory period (after an auditory cue indicating the*
 44 *target position, but prior to the start of the sound presentation) is shown separately for left and right*
 45 *parietal sensors in the left and right bottom panels, respectively. B) Adapted with permission from ¹³.*
 46 *Disruption of alpha lateralization when spatial attention is disrupted by a discontinuity in the target talker.*
 47 *Example stimuli are shown at the top for trials in which the nonspatial (talker) features of two competing*
 48 *speech streams are continuous (left) and when they switch, which, if it occurred, always was after the first*
 49 *two target syllables (right). Topographies show the normalized difference in alpha power when listeners*
 50 *focus attention to the left minus when they focus attention to the right (relative to the sum of the alpha power*
 51 *for attend-left plus attend-right), computed separately at each sensor on the scalp. Averages are computed*
 52 *from the moment of the potential talker switch to the end of the trial. The bottom bar graphs show the*
 53 *average normalized alpha change over the posterior left and posterior right channels computed from the*
 54 *scalp distributions. For switching trials, parietal alpha lateralization is weakened following the talker*
 55 *change.*

56 1.2 Talker discontinuity disrupts auditory spatial attention

57 Numerous behavioral studies demonstrate that maintaining attention on an ongoing auditory
 58 stream is supported by continuity of features like pitch, location, voice, and timbre^{21,22}. Feature
 59 continuity influences performance automatically: even when listeners know they should ignore
 60 some feature, such as talker identity, and attend to a different feature, such as location,
 61 discontinuities in the task-irrelevant feature disrupt attention^{21,23,24}. Indeed, effects of talker

62 continuity on speech perception in quiet have been ascribed to “talker normalization,” but may
63 actually be due to disruptions of attention triggered by a talker change^{25,26}.

64 Talker discontinuity during an auditory spatial attention task not only interferes with recall of the
65 target stream, it disrupts parietal alpha lateralization¹³ (see Figure 1B). In this recent study, two
66 competing speech streams were presented. Each syllable was presented from either left or right
67 and was spoken by either a male or a female. In *continuous* trials, the talker from each direction
68 was fixed throughout the trial, while in *switching* trials, the talkers switched locations after the first
69 two target syllables (see top of Figure 1B). In *switching* trials when listeners were instructed to
70 listen to syllables from one direction (ignoring any talker change), errors were elevated for the
71 syllable right after the talker switch—and alpha lateralization was disrupted (see bottom of Figure
72 1B). These results suggest that talker continuity overrides top-down, volitional control of spatial
73 attention and that talker discontinuity interrupts parietal alpha lateralization.

74 *1.3 Brain stimulation studies suggest a causal link between parietal alpha and visual* 75 *spatial attention*

76 Despite the strong association between alpha lateralization and spatial visual and auditory
77 attention, these results do not prove that parietal alpha “steers” attention. In humans, brain
78 stimulation methods such as transcranial magnetic stimulation (TMS) and transcranial electrical
79 stimulation (for reviews, see ^{27–30}) provide a means to directly test whether particular neural
80 regions are causally involved in particular behaviors.

81 TMS inactivation of parietal cortex in one hemisphere causes spatially specific visual processing
82 changes, enhancing spatial attention directed ipsilaterally but degrading it contralaterally³¹.
83 Unilateral TMS inactivation of the frontal eye field (FEF, part of the fronto-parietal visuo-spatial
84 attention network) reduces alpha coupling between prefrontal and parietal cortices; moreover,
85 parietal alpha lateralization is disrupted and this disruption predicts increases in reaction times
86 during a visual working memory task³². Unilateral 20-Hz rTMS (which disrupts alpha oscillations)
87 of either FEF or parietal cortex has similar effects³³. These stimulation studies confirm that the
88 fronto-parietal network is involved in controlling spatial attention, yet still beg the question: are
89 alpha oscillations causally responsible for suppressing contralateral information, or are they an
90 epiphenomenon?

91 Some studies have demonstrated effects of alpha-rate stimulation of parietal cortex on visual
92 perception using repetitive TMS (rTMS³⁴) or transcranial alternating current stimulation (tACS³⁵);
93 however, only a handful have addressed whether such stimulation affects spatial processing.
94 Alpha-rate rTMS of parietal cortex enhances performance for ipsilateral targets and degrades
95 performance for contralateral targets for visual spatial attention³⁶ and working memory³⁷ tasks,
96 while stimulation at non-alpha frequencies has no effect. Yet, tACS results are equivocal. Two
97 studies failed to find frequency- or retinotopically specific effects of parietal tACS stimulation on
98 visual tasks^{38,39}, while a high-density tACS (HD-tACS) found that parietal alpha stimulation
99 affects volitional control of visual spatial attention, improving performance for targets ipsilateral
100 to the stimulation⁴⁰.

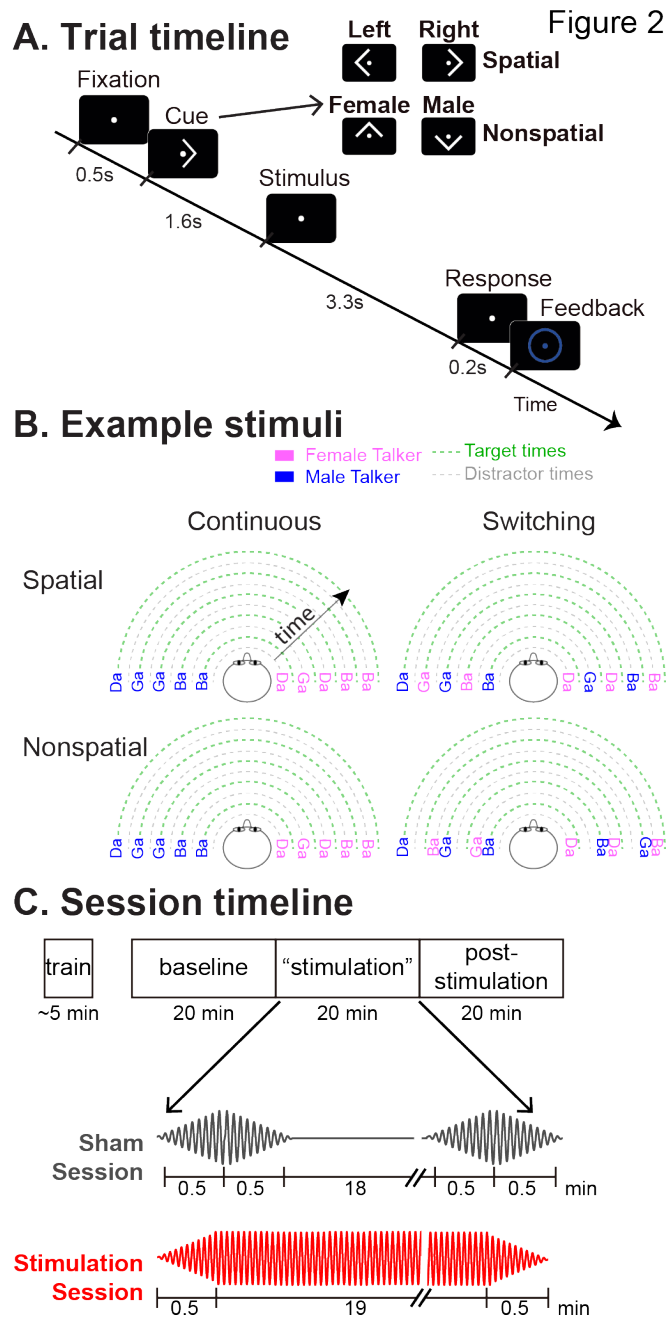
101 A few studies have shown that stimulation of auditory cortex can influence auditory task
102 performance⁴¹, including spatially specific effects on auditory selective attention^{42,43}. However,
103 we are unaware of any prior studies exploring whether parietal alpha stimulation influences
104 auditory spatial attention.

105 *1.4 Rationale of the current study*

106 Compared to traditional tACS (conducted through sponge pads), HD-tACS, which uses an
107 electrode ring configuration (e.g., an anode flanked by multiple cathodes), creates a more focused
108 electrical current sink^{44,45}. This allows for more precise anatomical targeting. Combined with
109 improved computational models of predicted current flow in the brain^{46,47}, HD-tACS yields more
110 precise brain stimulation than traditional approaches. We therefore used HD-tACS to achieve
111 focused, alpha-frequency stimulation of parietal cortex.

112 Our goal was to show that parietal alpha causally affects performance on a spatial auditory task in
113 a hemisphere-specific manner. Listeners focused attention on a stream of syllables while ignoring
114 a similar, competing stream. Our experimental design included multiple levels of controls designed
115 to test the specificity of stimulation effects on performance.

116 First, we expected alpha stimulation to only impact conditions where listeners volitionally focused
117 and could maintain spatial attention (and alpha lateralization). Listeners performed the same basic
118 task of focusing on a stream of spoken syllables, but focused either on location (spatial attention,
119 where parietal alpha HD-tACS should modulate performance) or talker gender (nonspatial
120 attention, where parietal stimulation should have no impact; see Figure 2A). On half of the trials
121 the talker from a particular direction remained fixed (*continuous* trials) and in the other half, the
122 talker alternated from syllable to syllable (*switching* trials; see Figure 2B). As discussed above, a
123 sudden spatial shift of talkers interferes with top-down spatial attention and disrupts alpha
124 lateralization¹³ (Figure 1B). Therefore, we expected alpha stimulation to have little effect on
125 *switching* trials, as talker discontinuities should exogenously disrupt spatial attention and parietal
126 alpha. We hypothesized that on *continuous* trials listeners would normally be able focus spatial
127 attention through alpha lateralization, so alpha stimulation would influence performance.



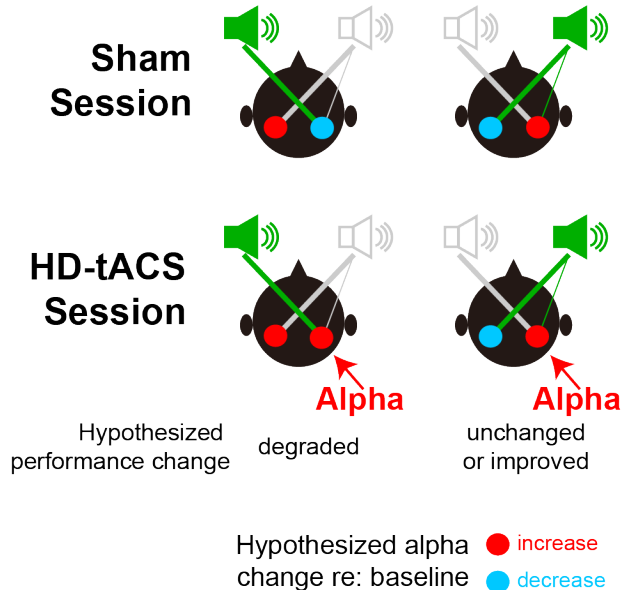
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129 *Figure 2. Task paradigm. A) Trial timeline. Subjects were instructed to foveate on a fixation dot appearing*
 130 *at the start of the trial. A visual cue then appeared, instructing them how to focus attention in the upcoming*
 131 *trial: left or right (a spatial trial) or male or female talker (a nonspatial trial). The target and distractor*
 132 *streams then began to play. Subjects were instructed to count the number of /ga/ syllables in the 5-syllable*
 133 *target stream. After the auditory stimulus, they were asked to report this count as quickly as possible.*
 134 *Following their response, a circle appeared around the fixation dot indicating whether they were correct*
 135 *or incorrect. B) Diagrams of example stimuli for the different trial types. The first syllable always was a*
 136 *distractor. Syllables were temporally interdigitated, alternating between distractor and target, in a*
 137 *temporally regular pattern. In continuous trials, the talker from each direction was fixed throughout the*

138 *trial. In switching trials, the talker from one direction alternated from syllable to syllable. C) Session*
139 *timeline. Following a brief training session, subjects performed three 20-min-long blocks of trials: pre-*
140 *stimulation baseline, “stimulation,” and post-stimulation. In Sham sessions, HD-tACS was ramped on and*
141 *off at the start and end of the “stimulation” block to blind subjects as to the condition. In Stimulation*
142 *sessions, HD-tACS ramped up at the start and down at the end of the “stimulation” block.*

143 Second, we stimulated parietal cortex unilaterally to test for spatial specificity of the stimulation.
144 We targeted right intraparietal sulcus (rIPS) based on previous findings suggesting that right
145 parietal cortex contains the only representation of left exocentric space, whereas right space is
146 represented strongly in left IPS but also weakly in rIPS^{1,48,49}. During spatial attention, we expected
147 rIPS alpha stimulation to suppress the representation of left exocentric space, impairing
148 performance for leftward targets (see Figure 3, bottom left panel). We had a secondary hypothesis
149 that performance for rightward targets might either be unchanged (as rIPS should already have
150 strong alpha due to top-down spatial attention) or enhanced (if stimulation lead to even better
151 suppression of the leftward distractor; see Figure 3, bottom right panel).

Figure 3 **Attend left Attend Right**



152

153 *Figure 3. Hypothesized alpha power in left and right parietal hemispheres, relative to baseline, during*
154 *spatial attention trials. The top row shows the expected patterns in Sham sessions, while the bottom row*
155 *shows the hypothesized effects of HD-tACS alpha stimulation of rIPS. Information is asymmetrical*
156 *represented; information from the left is represented only in the right (contralateral) parietal hemisphere,*
157 *while information from the right is represented most strongly in the left (contralateral) hemisphere, but*
158 *also weakly in the right hemisphere. In the absence of any stimulation (top row), top-down attention should*
159 *lead to a decrease in alpha power in the hemisphere contralateral to the direction of attention (allowing*
160 *the dominant representation of the attended location to be processed) and an increase in the ipsilateral*
161 *hemisphere (suppressing the dominant representation of the ignored location). We hypothesized that*
162 *applying alpha HD-tACS to rIPS should suppress the representation of leftward space, interfering with*
163 *processing of left targets (bottom left). However, alpha stimulation of rIPS should either have little effect,*
164 *or perhaps enhance processing of rightward targets, as rightward top-down attention already produces*
165 *strong alpha in rIPS (bottom right).*

166 Third, each subject performed two full sessions on separate days (order counter-balanced across
167 subjects). The Sham session applied transient currents to convince subjects that they were being
168 stimulated, while true HD-tACS was applied in the Stimulation session (see Figure 2C). The Sham
169 sessions thus provided a direct within-in subject control for the Stimulation sessions. Similarly,
170 each session began with a block of no-stimulation baseline trials, then presented a block of trials
171 with either HD-tACS or sham stimulation, and finally finished with a block of trials with no
172 stimulation (Figure 2C). We expected effects of HD-tACS stimulation to appear during the middle,
173 “stimulation” block, but to dissipate quickly, with performance in the no-stimulation block
174 returning to baseline.

175 Finally, to investigate frequency specificity, we conducted two experiments differing only in the
176 frequency of HD-tACS stimulation during the Stimulation session: alpha (10 Hz) in Experiment 1
177 and theta (6 Hz) in Experiment 2. We chose theta as a control frequency because, like alpha, theta
178 is an intrinsic oscillation occurring in parietal cortex^{50,51}, but one that is not linked to spatial
179 attentional control. Theta also closely neighbors the alpha band, making it a stringent control. We
180 hypothesized that alpha, but not theta, stimulation would affect spatial attention performance.

181 Our primary interest was to explore how HD-tACS stimulation influenced spatial attention. There
182 were two specific cases in Experiment 1 where we predicted a difference in performance between
183 the Sham and tACS sessions, each of which we expected to have a particular direction.
184 Specifically, during stimulation when listeners were using spatial attention for continuous stimuli,
185 we expected performance to be 1) worse in tACS than Sham sessions for leftward attention, but 2)
186 either better (or unchanged) in tACS than Sham sessions for rightward attention. We therefore
187 planned to conduct two signed planned comparisons, for these two conditions, a priori. We did not
188 expect any effects of theta stimulation in Experiment 2. Incidentally, we expected to replicate
189 previous results showing that talker switching interferes with spatial attention, a question we
190 addressed by comparing performance on continuous and switching trials for the initial block of
191 trials across all sessions, before stimulation.

192 **2 Results**

193 *2.1 Results confirm that talker switches exogenously interfere with spatial attention*

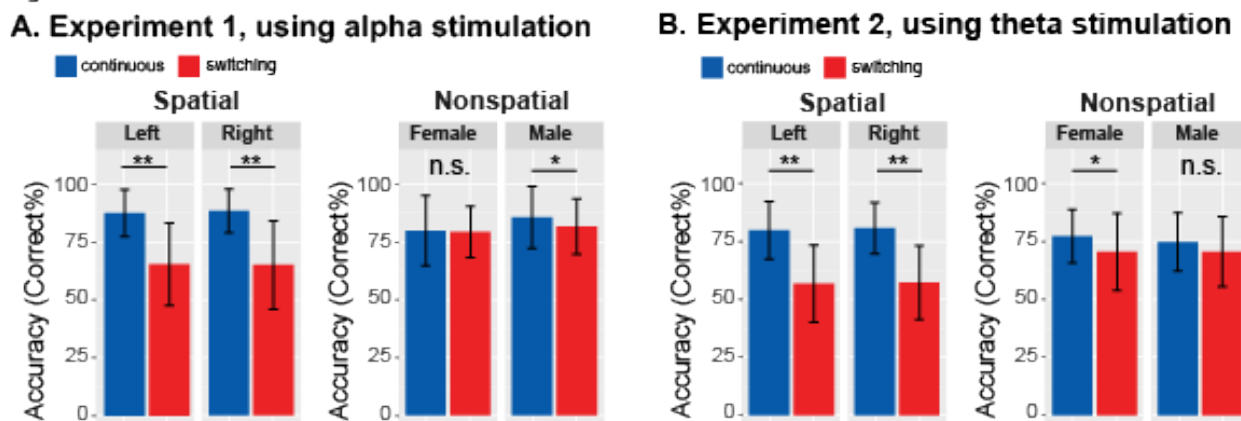
194 Based on previous results¹³, we expected performance to be worse in *switching* than *continuous*
195 trials, especially during spatial attention. Results confirmed this (see Figure 4). We averaged
196 performance for the baseline blocks of both the Sham and Stimulation sessions, since these blocks
197 were identical, occurring prior to any stimulation. We expected performance for these baseline
198 blocks to be similar in Experiments 1 and 2, since the trials in these blocks were identical across
199 the experiments (though the subjects differed). As seen in Figure 4, performance was worse in
200 *switching* trials than in *continuous* trials, especially during spatial attention, in both experiments.

201 Results from Experiment 1 are shown in Figure 4A. When listeners attended to the left,
202 performance changed in the expected direction, dropping from 87.40% correct in *continuous* trials
203 to 65.29% in *switching* trials ($Z_{(19)} = 3.91$, $P_{adj} < 0.001$, Wilcoxon signed rank test). When listeners
204 attended to the right, performance also dropped, from 88.27% for *continuous* to 64.81% for
205 *switching* trials ($Z_{(19)} = 3.90$, $P_{adj} < 0.001$). When listeners directed attention to a specific talker,

206 the average accuracy also dropped slightly for *switching* compared to *continuous* trials for both
 207 attend-female (79.62% to 79.13%) and attend-male (85.48% to 81.44%) trials. For attend-female
 208 trials, this change was not significant ($Z_{(19)} = 0.20$, $P_{adj} > 0.99$); however, it did reach significance
 209 for attend-male trials ($Z_{(19)} = 2.36$, $P_{adj} = 0.036$).

210 Results from Experiment 2, shown in Figure 4B, were similar. When listeners attended to the left,
 211 performance dropped as expected, from 79.81% correct in *continuous* trials to 56.84% correct in
 212 the *switching* trials ($Z_{(17)} = 3.66$, $P_{adj} < 0.001$, Wilcoxon signed rank test corrected for multiple
 213 comparisons). When listeners attended to the right, performance dropped from 80.77% to 57.26%
 214 ($Z_{(17)} = 3.71$, $P_{adj} < 0.001$). When listeners directed attention to a specific talker, average accuracy
 215 was lower for *switching* than *continuous* trials for both attend-female (77.35% to 70.51%) and
 216 attend-male (74.79% to 70.62%) trials. This change reached statistical significance for the attend-
 217 female trials ($Z_{(17)} = 2.76$, $P_{adj} = 0.011$), but not the attend-male trials ($Z_{(17)} = 1.86$, $P_{adj} = 0.13$).

Figure 4



218
 219 *Figure 4. Behavioral performance averaged across baseline blocks in which there was no stimulation.*
 220 *Talker switching significantly disrupts spatial attention, but not nonspatial attention. A. Results from*
 221 *Experiment 1. The left plot shows results for spatial attention, comparing continuous and switching trials;*
 222 *the right plot shows results for nonspatial attention. Error bars represent the across-subject standard error*
 223 *of the means. Double asterisks indicate statistical differences with $p < 0.001$. B. Results from Experiment*
 224 *2, laid out as in A.*

225 It is worth noting that our talker switched after each syllable (see Figure 2B), which should be
 226 more disruptive than a single switch (as in ¹³, which inspired this manipulation). Consistent with
 227 this, we found a larger drop in performance from *continuous* to *switching* trials than in ¹³.

228 2.2 Baseline performance is similar in Sham and Stimulation sessions

229 Each subject in both experiments performed both a Sham and a HD-tACS Stimulation session.
 230 Session order was randomized and counter-balanced across subjects, who were blinded to this
 231 aspect of the experimental design. In both Sham and Stimulation sessions, the first trial block was
 232 a no-stimulation, baseline block.

233 We first confirmed that there was no significant difference in baseline performance between Sham
 234 and Stimulation sessions in either Experiment 1 ($Z_{(19)} = 0.068$, $P = 0.95$, Wilcoxon rank test) or

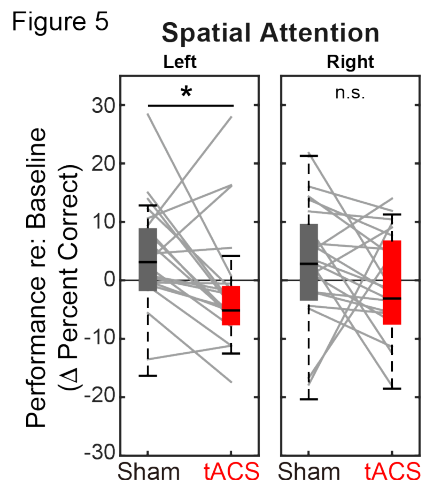
235 Experiment 2 ($Z_{(17)} = 0.46$, $P = 0.65$, Wilcoxon rank test). Thus, counter-balancing the session
236 order cancelled out any systematic effects of testing order.

237 To correct for changes in individual performance between sessions, we referenced performance to
238 that in the baseline block in each session. To test whether our results could be confounded by
239 performance fluctuations in this baseline level between test days, we performed test – retest
240 reliability analyses, comparing baseline results across different testing days⁵². We found that
241 individual subjects’ performance across sessions were significantly correlated in both Experiment
242 1 (Spearman’s $R_{hos} = 0.48$; $P = 0.032$) and Experiment 2 (Spearman’s $R_{hos} = 0.52$; $P = 0.028$),
243 indicating the stability of individual differences across testing days.

244 2.3 Alpha HD-tACS of rIPS disrupts auditory spatial attention for leftward targets

245 We first conducted a within-subject comparison of baseline-corrected performance in Sham and
246 Stimulation sessions for trials where we expected an effect. We analyzed only *spatial* trials, since
247 parietal processing is not involved during nonspatial attention. Similarly, having confirmed that
248 talker discontinuities disrupted top-down spatial attention (see Figure 4), we restricted this initial
249 analysis to *continuous* trials. Finally, we expected any effects to be present during, but not after
250 stimulation. Thus, a priori, we considered only two of the many conditions tested; the full set of
251 control trials from Experiment 1 and results from control Experiment 2 are shown in the next
252 section.

253 We predicted stimulation to decrease performance for leftward spatial attention compared to the
254 Sham session, but either to increase or have no effect for rightward spatial attention. Results
255 confirmed these expectations. The rIPS HD-tACS alpha stimulation disrupted performance for
256 leftward spatial attention (contralateral to the stimulated hemisphere), but produced no significant
257 effect for rightward attention (ipsilateral to the stimulation; see Figure 5A). Specifically, for rIPS
258 alpha stimulation, performance in the “stimulation” block was significantly worse in the
259 Stimulation session than in the Sham session for left attention ($Z_{(19)} = 2.10$, $P_{adj} = 0.036$, Wilcoxon
260 signed rank test, corrected for multiple comparisons). There was no significant increase in
261 performance from Sham to Stimulation sessions for right attention ($Z_{(19)} = 1.27$, $P_{adj} > 0.99$; see
262 Figure 5A). For the left-attention trials, the effect size of stimulation was 0.33, computed using the
263 z value obtained from the Wilcoxon test with the formula: $d = z/\sqrt{N}$ ⁵³.



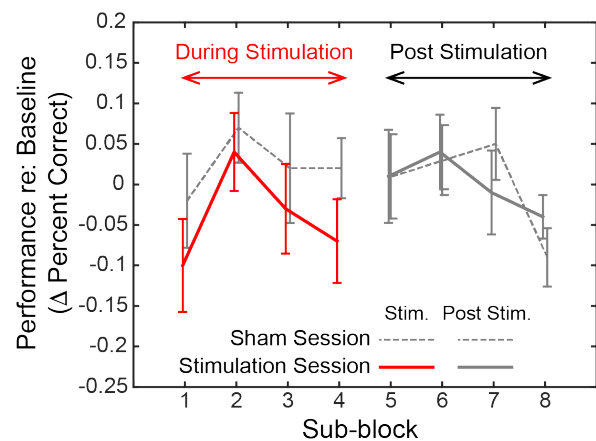
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265 *Figure 5. Baseline-corrected performance for spatial attention trials in the “stimulation” blocks,*
266 *comparing Sham and Stimulation sessions. Parietal HD-tACS stimulation shows spatially specific and*
267 *frequency-specific effects. Compared to Sham stimulation, rIPS alpha HD-tACS stimulation significantly*
268 *impaired performance on attend-left trials, but had no effect on attend-right trials.*

269 We next explored the dynamics of the effect of alpha stimulation on spatial attention to leftward
270 targets. For both the Sham and the Stimulation sessions, we subdivided both the “stimulation”
271 block and the post-stimulation block into 4 sub-sessions (each comprising 6 spatial, attend-left
272 trials) and computed the baseline-corrected performance for each (Figure 6).

273 We observed a consistent, sustained effect of stimulation: baseline-corrected performance was
274 lower in the Stimulation session compared to the Sham session for each of the sub-blocks in the
275 “stimulation” block (left side of Figure 6). This difference disappeared by the first post-stimulation
276 sub-block, immediately after HD-tACS stopped; baseline-corrected performance was
277 indistinguishable for the Sham and Stimulation sessions for the final four sub-blocks (right side of
278 Figure 6).

Figure 6



279

280 *Figure 6. Dynamics of the effect of rIPS alpha HD-tACS stimulation on spatial, attend-left trials, comparing*
281 *Sham and Stimulation sessions. Performance is consistently poorer for alpha stimulation than for sham*

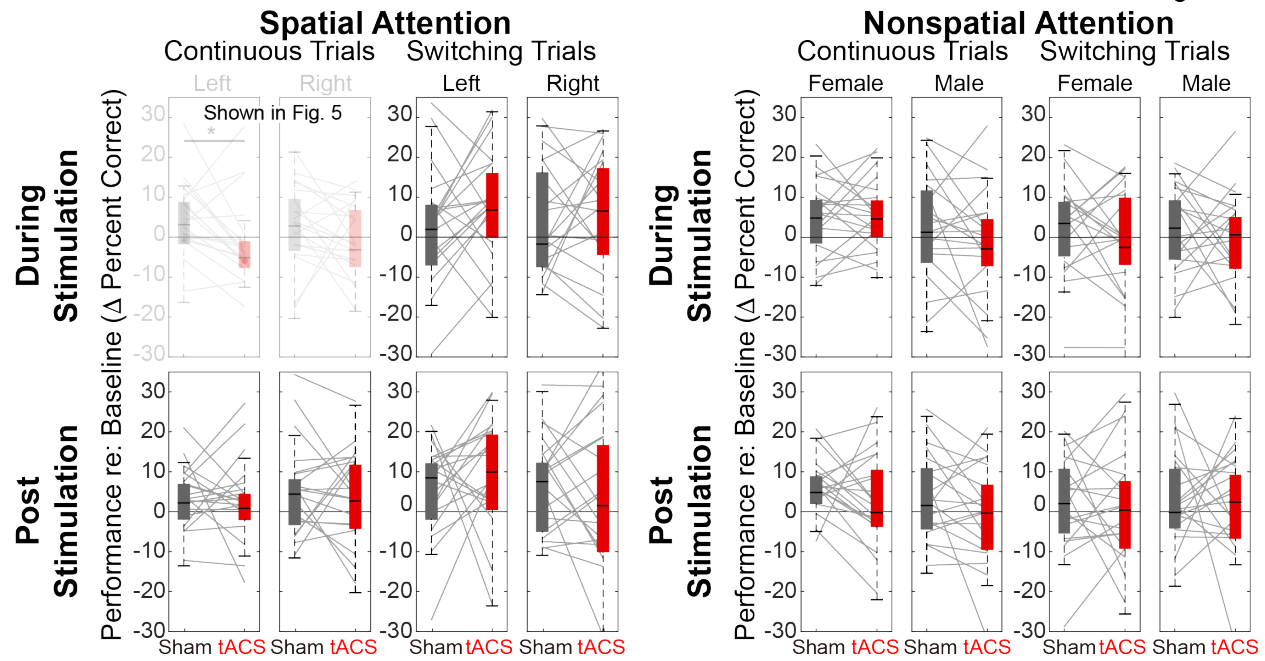
282 *stimulation throughout the course of stimulation; however, performance in the sessions is indistinguishable*
283 *once stimulation ends. Trials within both the “stimulation” block and post-stimulation block were divided*
284 *into 4 sub-blocks each. Baseline-corrected performance and the standard error of the mean across subjects*
285 *are shown for the Sham and the Stimulation sessions (dashed and solid lines, respectively). Data from the*
286 *“true” stimulation sub-blocks are shown in red (the first four sub-blocks of the Stimulation session); no-*
287 *stimulation sub-blocks are shown in gray (all sub-blocks of the Sham session, as well as the final four sub-*
288 *blocks of the Stimulation session).*

289 **2.4 Theta, stimulation does not affect performance during spatial attention**

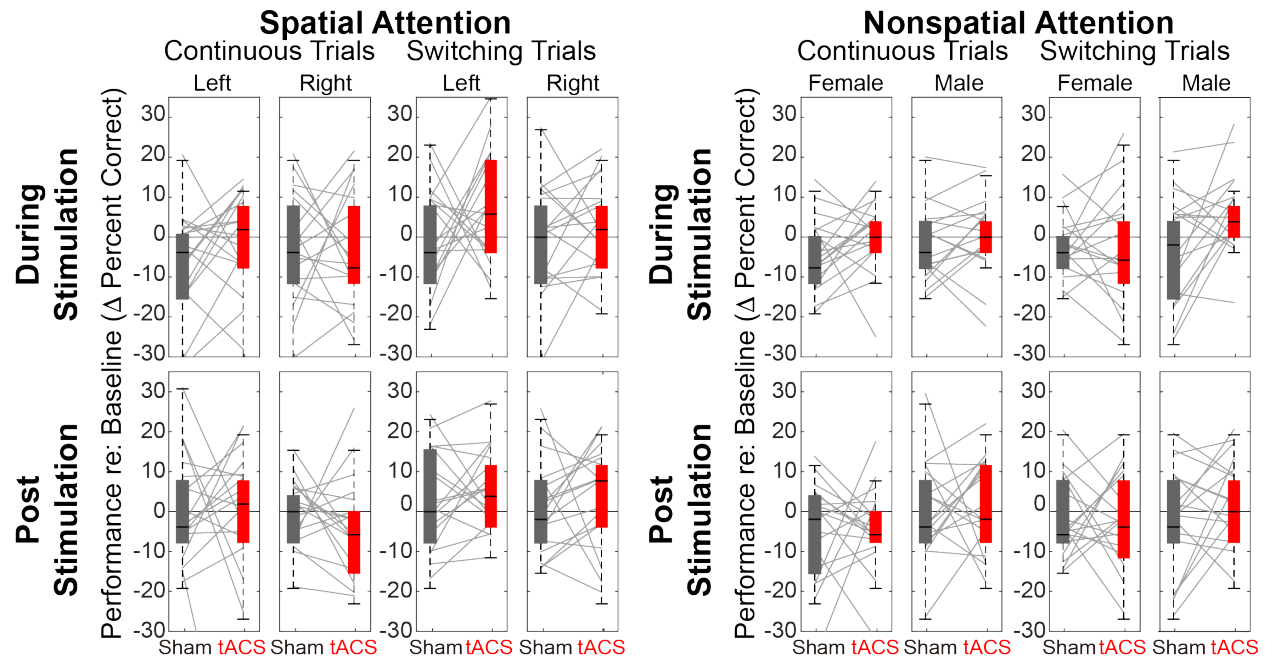
290 Figure 5A demonstrates that there is a spatially specific effect of HD-tACS stimulation. We
291 included a number of other control conditions where we expected no effects of stimulation (see
292 Figure 7).

A. Experiment 1, using alpha stimulation

Figure 7



B. Experiment 2, using theta stimulation



293

294 *Figure 7. Comparison of Sham and Stimulation session results. There is no effect of stimulation in any of*
 295 *the control conditions. (Note that the top left panels in A. are repeated from Figure 5). A. Results from*
 296 *Experiment 1, using alpha HD-tACS. Results for spatial attention are shown on the left, and for nonspatial*
 297 *attention shown on the right. For each form of attention, results are broken down into continuous and*
 298 *switching trials (two leftmost and two rightmost panels, respectively). For spatial attention, results are*
 299 *shown for both attend-left and attend-right trials; for nonspatial attention, results are shown for attend-*
 300 *female and attend-male trials. Finally, results from trials during the “stimulation” block are shown in the*

301 top row and from the subsequent post-stimulation block in the bottom row. B. Results from Experiment 2,
 302 using theta stimulation, laid out as in A.

303 Theta stimulation (Experiment 2) was not expected to alter parietal processing for any trials (all
 304 panels in Figure 7B). Because parietal cortex should not be strongly engaged during nonspatial
 305 attention, we expected no stimulation effects in any of the nonspatial attention trials (right half of
 306 Figures 7A and 7B). We expected the effects of stimulation to dissipate rapidly, with no residual
 307 effect in the post-stimulation block (bottom rows in Figures 7A and 7B). Because talker switches
 308 exogenously disrupt spatial attention (and, likely, parietal alpha; 16), we expected no influence of
 309 stimulation during *switching* trials, even in spatial-attention trials (third and fourth panels of the
 310 top row in Figures 7A and 7B). These expectations were all borne out by our results.

311 Of the 32 distinct trial types, Sham vs. Stimulation sessions differed significantly only in one, in
 312 the expected direction: during alpha stimulation of rIPS, when listeners directed spatial attention
 313 to a continuous-talker target that was on the left (top leftmost panel in Figure 7A, repeated from
 314 Figure 5A). Table 1 shows the results of statistical tests directly comparing Sham and Stimulation
 315 baseline-corrected results for all trial types in Experiment 1 (Wilcoxon rank tests). In addition, there
 316 was no effect of theta stimulation for any of the 16 trial types [(spatial and nonspatial attention) x
 317 (during stimulation and post stimulation) x (continuous trials and switching trials) x (left/female
 318 and right/male)]: for all of these, $Z_{(17)} < 1.67$ ($P > 0.095$).

Experiment 1, using alpha stimulation								
	Spatial Attention				Nonspatial Attention			
	Continuous		Switching		Continuous		Switching	
	Left	Right	Left	Right	Female	Male	Female	Male
During Stimulation	$Z = 2.10$ $P_{adj} = 0.036$	$Z = 1.27$ $P_{adj} = 1$	$Z = 1.21$ $P = 0.23$	$Z = 0.58$ $P = 0.56$	$Z = 0.11$ $P = 0.91$	$Z = 1.08$ $P = 0.28$	$Z = 0.69$ $P = 0.49$	$Z = 0.71$ $P = 0.48$
Post Stimulation	$Z = 0.87$ $P = 0.39$	$Z = 0.23$ $P = 0.82$	$Z = 1.03$ $P = 0.30$	$Z = 0.66$ $P = 0.51$	$Z = 1.02$ $P = 0.31$	$Z = 0.98$ $P = 0.33$	$Z = 0.33$ $P = 0.74$	$Z = 0.10$ $P = 0.92$

319 Table 1. Statistical tests comparing baseline-corrected performance in Sham and Stimulation sessions for
 320 the various types of control trials in Experiment 1, laid out as in Figure 7A. Each cell represents results of
 321 a Wilcoxon rank test with 19 degrees of freedom. Note that the primary comparisons of interest (left vs.
 322 right spatial attention for continuous stimuli during rIPS alpha stimulation; results shown in light gray)
 323 were already discussed in Section 2.3.

324 In Experiment 1 where we imposed alpha HD-tACS rIPS, we further examined performance for
 325 the *continuous* nonspatial trials, which presented stimuli that were physically identical to those for
 326 where we saw stimulation effects (*continuous* trials during spatial attention). We reanalyzed
 327 performance for the *continuous* nonspatial trials by collapsing across the direction of the target (a
 328 feature that listeners were presumably ignoring), regardless of the gender of the target talker (the
 329 feature that listeners were presumably attending) and examining performance for leftward and
 330 rightward targets. If parietal stimulation disrupted attention for leftward, continuous targets when
 331 attention was directed to talker gender, it would suggest that spatial parietal processing contributed
 332 to performance even during nonspatial attention trials. Comparing baseline-corrected performance
 333 for Sham vs. Stimulation sessions during nonspatial attention, we observed no effect of stimulation
 334 for targets from either the left ($Z_{(19)} = 0.23$, $P = 0.82$) or the right ($Z_{(19)} = 1.30$, $P = 0.19$). These

335 results further support the view that alpha stimulation of parietal cortex only influences top-down
336 spatial processing.

337 **3 Discussion**

338 *3.1 Summary of Results*

339 Using HD-tACS to stimulate rIPS, we here show a causal relationship between parietal alpha
340 power and spatial auditory attention. Our study design was rigorous, with numerous controls to
341 establish the specificity of the influence of parietal alpha. We used a within-subject design that
342 included counterbalanced Sham and Stimulation sessions, and that employed both baseline and
343 post-stimulation control blocks within each session to control for performance fluctuations and to
344 validate the internal consistency of the behavioral metrics. We found that HD-tACS parietal
345 stimulation disrupted selective attention performance only when listeners focused top-down
346 attention based on spatial features, not talker identity; only when the target stream from the
347 attended direction was consistent, not when the talker switched abruptly; only when attention was
348 directed to a location contralateral to the parietal hemisphere being stimulated, not for ipsilateral
349 targets; and only for alpha, not theta stimulation.

350 In our study, alpha HD-tACS stimulation produced an effect size of 0.39 for leftward spatial
351 attention. A meta-analysis study⁵⁴ shows that this effect size is comparable to those in past
352 published reports of tACS effects on cognitive function in healthy adults ($\bar{E} = 0.36$, 95% $CI =$
353 $0.27-0.46$) as well as tDCS studies (e.g., $\bar{E} = 0.23$, 95% $CI = 0.09-0.36$)⁵⁵⁻⁵⁷. Thus, we not only
354 established a very specific role of parietal alpha in auditory selective attention, the effect is as
355 robust as other reported effects of neural stimulation.

356 *3.2 Spatial and frequency specificity show that parietal alpha causally influences*

357 *auditory spatial attention*

358 We performed two experiments identical in every aspect except for the frequency of HD-tACS
359 stimulation; Experiment 1 used HD-tACS in the alpha band (10 Hz), while Experiment 2
360 stimulation was at a closely neighboring theta frequency (6 Hz). We found no evidence that theta
361 stimulation altered performance. This frequency specificity of HD-tACS parietal stimulation
362 implicates alpha in control of auditory spatial attention.

363 Given that parietal cortex dominantly represents contralateral space, we expected alpha stimulation
364 of one parietal hemisphere to affect spatial attention differently for ipsilateral and contralateral
365 targets. Specifically, we expected rIPS stimulation to impair performance when listeners would
366 otherwise have successfully focused spatial attention to the left (see Figure 3). In contrast, we
367 expected stimulation to either produce no effect or perhaps improve performance on attend-right
368 trials. We found that stimulation interfered with spatial attention to leftward sources, but had no
369 significant effect for rightward sources.

370 The lack of an effect rather than improvement for rightward spatial attention could arise for a few
371 reasons. First, previous visual attention studies show that alpha-tACS increases endogenous alpha

372 oscillations only when alpha power is low^{58,59}. Top-down attention to the right should naturally
373 produce strong rIPS alpha, limiting the influence of additional alpha power (see Figure 3). In
374 contrast, rIPS alpha power should be low during leftward attention, allowing stimulation to have
375 a large impact. Second, parietal cortex is asymmetrical; rIPS dominantly represents left space, but
376 also has a weak representation of right space. When listeners attended to the right, an injection of
377 alpha energy to rIPS may have enhanced suppression of the dominant leftward distractor, but it
378 may also have spread to suppress the weak representation of the rightward target, leading to little
379 net change. Regardless, the spatial specificity of the effect of rIPS stimulation is consistent with
380 the hypothesis that parietal alpha causally suppresses the representation of contralateral space,
381 steering spatial attention.

382 *3.3 Task-specificity and stimulus-specificity show that parietal alpha stimulation* 383 *influences volitional spatial attention, but not exogenous attention*

384 Past studies demonstrate that spatial auditory attention and working memory engage parietal
385 processing, whereas attending to the same acoustic source using nonspatial attention does not^{5,18–}
386 ²⁰. We therefore hypothesized that top-down focus of auditory attention would be affected by HD-
387 tACS stimulation for spatial, but not nonspatial, auditory attention. Consistent with our
388 expectations, we found no effect of parietal stimulation when listeners directed attention based on
389 talker gender. To further check that rIPS stimulation did not impact nonspatial attention, we
390 analyzed nonspatial attention performance for *continuous* targets that happened to be from the left
391 – physically identical to the stimuli for which rIPS HD-tACS alpha stimulation impaired spatial
392 attention performance. As expected, HD-tACS stimulation had no significant impact on nonspatial
393 attention.

394 In *switching* stimuli, the irrelevant target feature alternated from syllable to syllable. Based
395 previous results¹³, we postulated that talker switches would cause exogenous, involuntary
396 disruptions of spatial attention and of parietal alpha lateralization. We further expected these
397 exogenous interruptions to override top-down, parietal influences on spatial focus, rendering
398 parietal stimulation irrelevant. Behaviorally, we verified that *switching* stimuli impaired spatial
399 attention performance. We also found, as expected, no evidence that rIPS alpha stimulation affects
400 perception when parietal alpha lateralization is already disrupted by talker discontinuities in the
401 attended direction.

402 Thus, our results show that parietal alpha stimulation influences top-down spatial attention, but
403 not top-down attention to a particular talker, even for the same physical sound mixture and the
404 same target stream. Further, when exogenous attention involuntarily overrides the top-down
405 control of spatial attention, external alpha parietal stimulation is ineffective. Together, these
406 findings implicate parietal alpha in volitional steering of auditory spatial attention.

407 *3.4 Our results confirm and clarify past results from visual attention studies*

408 As noted in the Introduction, past studies exploring how parietal alpha stimulation influences
409 performance have produced apparently conflicting results. Alpha rTMS of parietal cortex increases
410 performance for ipsilateral targets and decreases performance for contralateral targets, both in
411 visual attention and visual working memory tasks, while no effects are found for other stimulation

412 rates^{36,37}. However, past results from the handful of studies that used tACS to stimulate parietal
413 cortex during visual spatial attention are less conclusive.

414 One study directly compared unilateral sham, 6-Hz, 10-Hz, and 25-Hz tACS stimulation of parietal
415 cortex³⁸, but found no retinotopic specificity of stimulation and only weak frequency specificity
416 during a visual detection task. Another tACS study found that right parietal stimulation shifted the
417 perception of the midpoint of a line segment while sham stimulation did not; however, a follow up
418 experiment in the same study failed to replicate the initial finding, with no significant effect of
419 sham or alpha stimulation³⁹.

420 While these two studies seem to suggest that lateralized parietal alpha may not causally steer visual
421 spatial attention, a more recent study offers a more nuanced explanation. Schumann and
422 colleagues⁴⁰ compared the effects of HD-tACS alpha stimulation of left parietal cortex for three
423 visual tasks: a *detection* task, an *exogenous* spatial attention task, and an *endogenous* spatial
424 attention task. Stimulation had no effect on *detection* of a faint visual grating. In the spatial
425 attention tasks, observers had to not just detect, but also report the orientation of the grating. In the
426 *exogenous attention* task, four dots appeared around one of the potential target positions and the
427 target either appeared in that position (congruent; 50% of the trials) or in the opposite hemifield
428 (incongruent; 50% of the trials). Observers were better in congruent than incongruent trials—but,
429 critically, parietal stimulation had no impact on performance. Finally, in the *endogenous attention*
430 task, a visual cue correctly indicated the location of a subsequent target on 80% of the trials,
431 providing a top-down cue for spatial attention. In this case, and only this case, parietal alpha
432 stimulation caused a spatially specific effect, decreasing reaction times for ipsilateral targets.

433 These findings highlight the importance of carefully considering task demands when interpreting
434 results of parietal stimulation studies. While parietal alpha modulates volitional control of spatial
435 attention tasks, it does not robustly influence *exogenous* attention. The sudden appearance of a
436 new stimulus, even one near threshold, may draw exogenous attention⁶⁰, which may override any
437 effects of parietal processing and render alpha parietal stimulation impotent³⁸.

438 In addition, whereas Schumann and colleagues used HD-tACS, the studies that failed to see
439 consistent, spatially specific effects of parietal alpha stimulation used traditional tACS. Traditional
440 tACS is usually delivered with large pads (20-30cm²) and stimulates a broad area between the
441 stimulation electrodes^{46,61}. The resulting spread of electric current is greater, and could even spread
442 to both hemispheres, confounding stimulation effects.

443 3.5 Our study differs from past brain stimulation studies in audition

444 As noted in the Introduction, a few studies stimulated auditory cortex and demonstrated behavioral
445 effects⁴¹⁻⁴³. However, we know of no other studies that show a causal influence of parietal alpha
446 oscillations on auditory spatial attention.

447 The most closely related study used traditional tACS to target a large region of left hemisphere
448 that included portions of temporal and inferior parietal cortices⁴². This study shows a double-
449 dissociation between stimulation at alpha vs. gamma frequencies; specifically, alpha stimulation
450 degrades attention to contralateral stimuli, while gamma stimulation improves contralateral
451 attention.

452 In contrast to their study, our HD-tACS stimulation targeted intraparietal sulcus and produces
453 essentially no current in auditory sensory regions (see Fig. 8C). The two studies are consistent in
454 showing that alpha stimulation impairs attention to contralateral auditory space. However, ours
455 demonstrates that alpha in IPS, which is a part of the well-studied visuo-spatial attention network,
456 plays a causal role in spatial auditory attention, whereas the effects reported by Wöstmann and
457 colleagues could be due to stimulation of auditory sensory regions. In addition, by including a
458 nonspatial attention task as a control, we also show that the influence of IPS alpha depends
459 specifically on top-down engagement of the visuo-spatial attention network; there is no influence
460 of IPS alpha stimulation when listeners attend to the same auditory source within the same physical
461 sound mixture, but do so using nonspatial auditory features. Additional studies are needed to
462 replicate and confirm our results, and to further delineate the conditions under which parietal alpha
463 influences auditory perception.

464 The above studies explored the effect of alpha tACS on visual spatial processing. Yet, we believe
465 that auditory spatial attention recruits the same fronto-parietal network involved in visual spatial
466 attention⁵ (see the discussion in ²⁰). We therefore expect manipulation of parietal alpha to lead to
467 similar effects for auditory spatial attention and visual spatial attention. Consistent with ⁴⁰, we used
468 alpha HD-tACS to focally stimulate parietal cortex. As in their study, we found that manipulation
469 of parietal alpha affects control of *endogenous* spatial attention (processing of *continuous*
470 contralateral targets during a spatial attention task)—but does not influence performance
471 dominated by *exogenous* attention effects (processing of *switching* targets, where *endogenous*
472 disruptions limit performance).

473 3.6 Caveats and Future Work

474 We know of no other studies that show a causal influence of parietal alpha oscillations on auditory
475 spatial attention. Additional studies are needed to replicate and confirm our results, and to further
476 delineate the conditions under which parietal alpha influences auditory perception.

477 We used HD-tACS to achieve relatively precise control of the spatial distribution of brain
478 stimulation. However, even with this approach, the induced current intensity is not uniformly
479 distributed throughout rIPS (see Figure 8). IPS is both narrow and relatively long. The estimate of
480 the stimulation we delivered suggests the strongest stimulation arises in the most posterior regions
481 of IPS (IPS1 and IPS2⁴); however, auditory spatial attention relies primarily on higher IPS
482 regions⁵. Additional studies should be undertaken that more precisely target areas engaged by
483 auditory spatial attention, for instance, by designing HD-tACS stimulation using current flow
484 modelling based on each individual subject's anatomy.

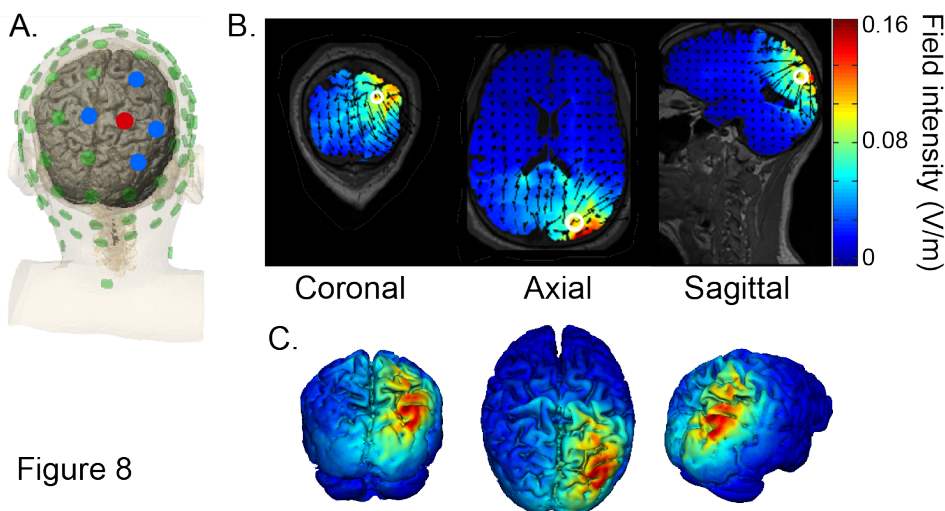


Figure 8

485

486 *Figure 8. HD-tACS model, targeting rIPS. A. Diagram of the electrode montage. Five parietal channels*
487 *(CP2, P2, P4, Pz, POz) were selected from a standard 64-channel EEG cap. The blue and red dots,*
488 *indicating opposite polarities, show the chosen stimulation polarity distribution. This distribution produces*
489 *a current sink targeting right intraparietal sulcus (IPS). B. The current flow model based on the selected*
490 *montage, showing 2D coronal, axial and sagittal views of the stimulation reaching each position in the*
491 *brain. The open white circle indicates the targeted Montreal Neurological Institute coordinate (24, -70,*
492 *41), based on a previous fMRI study that mapped the location of human IPS⁴. C. Three views of the 3D*
493 *model simulation.*

494 There is no consensus as yet on whether or not tACS induces neural entrainment that persists
495 beyond the period of active stimulation⁶². Some human studies report tACS after-effects that
496 persist as long as 40 min^{63–65}. In vivo animal studies show that neural entrainment ceases as soon
497 as stimulation stops^{66,67}; yet, animal studies also generally use briefer stimulation periods, which
498 may reduce the duration of any after-effects⁶⁸. In our study, the effects of HD-tACS did not persist
499 into post-stimulation testing (Figure 6). It may be that more intense stimulation would elicit an
500 after-effect⁶⁹. Alternatively, alpha stimulation effects may be more prominent and after-effects
501 more long-lasting when the exact frequency of stimulation is matched to the individual subject's
502 natural peak alpha frequency⁴⁵. Future work is needed to map out the physiological foundations of
503 tACS and the relationship between stimulation effectiveness, effect duration, and tACS parameters
504 such as current intensity and frequency.

505 While we were able to degrade attention to sounds contralateral to the stimulation site, we did not
506 find enhancement of ipsilateral attention; however, we did not match our stimulation to individual
507 participants' alpha frequency. Closed-loop methods that match the frequency of stimulation to
508 endogenous neural oscillations in real-time may provide more robust changes in brain function,
509 enhancing information processing and improved performance, which could open up an entirely
510 new realm of treatment options for cognitive brain disorders.

511 The present findings add to a growing body of neuromodulation research addressing the
512 importance of rhythmic neural information in health and disease. Abnormalities in parietal alpha
513 and its distribution across cerebral hemispheres has been documented in numerous disorders (e.g.,
514 Alzheimer's disease⁷⁰, depression⁷¹ and ADHD⁷²). Studies like ours, which directly manipulate
515 oscillatory parietal activity, lay critical groundwork for development of interventions to alleviate

516 problems due to atypical cortical mechanisms in a range of neurological and neuropsychiatric
517 disorders.

518 **4 Methods**

519 *4.1 Subjects*

520 Thirty-eight volunteers gave written consent to procedures approved by the Boston University
521 Institutional Review Board. The subjects were paid for their participation. Twenty volunteers aged
522 between 18-24 years (mean 21.15 yr., standard deviation 3.01 yr.; 13 females, 7 males) participated
523 in Experiment 1. Eighteen volunteers aged between 18-24 years (mean 22.11 yr., standard
524 deviation 2.4 yr.; 15 females, 3 males) participated in Experiment 2. All participants had clinically
525 normal audiometric thresholds in both ears for frequencies from 250 Hz to 8k Hz (thresholds less
526 than 20 dB HL).

527 We conducted a pilot experiment with six subjects and estimated an effect size for the “attend left,
528 continuous, spatial attention” trials during alpha stimulation of right parietal cortex. Given that we
529 also planned on testing “attend right, continuous, spatial attention” trials, we estimated that we
530 needed 16 subjects to achieve a power of 0.8 (correcting for multiple comparisons). Because we
531 anticipated some attrition, we recruited 20 subjects in Experiment 1 and 18 in Experiment 2, all of
532 whom completed the experiments.

533 *4.2 Task and Stimuli*

534 Subjects performed a selective auditory attention task, diagrammed in Figure 2A. At the beginning
535 of each trial, subjects fixated their gaze on a dot presented at the center of a computer screen. A
536 visual cue starting 0.5 s later (0.4 s duration) instructed subjects which of two competing speech
537 streams to attend, based on either *spatial* or *nonspatial* features. In *spatial* trials, the cue was either
538 a left or right arrow, indicating the location of the target speech stream. In *nonspatial* trials, the
539 cue was either an up or down arrow, indicating the gender of the target stream talker (female or
540 male talker). The sound stimuli began 1.2 s after the visual cue disappeared and lasted 2.3 s.
541 Listeners had one second after this to enter their response on the keyboard, at which point a colored
542 circle appeared around the fixation dot for 0.2 s to indicate if the response was correct (blue) or
543 incorrect (red). Cash bonus was given to subjects for each trial correctly answered within the time
544 limit.

545 In each trial, sound stimuli comprised two competing speech streams: a target and a distractor.
546 Both target and distractor streams were five syllables long. The syllables were chosen from the
547 same set of voiced-stop-consonant-vowel utterances (/ba/, /da/, and /ga/; each 388 ms in duration)
548 recorded by one female talker and one male talker (F0 roughly 189 Hz and 125 Hz, respectively,
549 as estimated by Praat software). Each syllable was spatialized to be perceived as either 90 degrees
550 to the left or 90 degrees to the right by convolving raw recordings with manikin head-related
551 transfer functions⁷³. Both the target stream and the distractor stream were isochronous, with an
552 inter-syllable interval of 433 ms. However, the two streams were temporally interdigitated: the
553 distractor stream always began first, 180 ms before the target stream.

554 On each trial, the listener's goal was to count the number of /ga/ syllables in the target stream,
555 which was either defined by its location in *spatial* trials (left or right, chosen randomly on each
556 trial with equal likelihood) or its talker in *nonspatial* trials (male or female, chosen randomly on
557 each trial with equal likelihood). The task-irrelevant feature (talker in *spatial* trials; location in
558 *nonspatial* trials) was either consistent throughout the stream (*continuous* trials) or changed from
559 syllable to syllable within both the target stream and the distractor stream (*switching* trials; see
560 Figure 2B). Each trial was pseudo-randomly chosen to be either *spatial* or *nonspatial* and either
561 *continuous* or *switching*. Therefore, to perform the task listeners had to focus attention on the task-
562 relevant dimension for that trial and try to ignore the task-irrelevant dimension. The five syllables
563 making up each stream were randomly chosen with replacement, subject to the further constraint
564 that no syllable was the same as the syllable just prior to it or just after it (which were always in
565 the competing stream).

566 Stimuli were presented via earphones (ER-2, Etymotic Research, Inc.) in a double-walled Eckel
567 sound-treated booth at Boston University. All sound stimuli were presented at a sound pressure
568 level of approximately 75 dB.

569 4.3 Experimental Procedures

570 We conducted two experiments, differing in the form of HD-tACS stimulation that was applied to
571 right parietal cortex. In Experiment 1, HD-tACS stimulation was at a frequency in the middle of
572 the alpha range (10 Hz), while in Experiment 2, it was in the theta frequency range (6 Hz). Other
573 than this detail, the two experiments were procedurally identical.

574 In each experiment, each subject performed two experimental sessions on two different days: a 1.5
575 mA HD-tACS Stimulation session and a Sham control session. The order of the Stimulation and
576 Sham sessions was counterbalanced across subjects. In Experiment 1, the two testing days were
577 separated by 1-14 days (mean of 2.45 days; standard deviation of 3.12 days). In Experiment 2, the
578 two testing days were separated by 1-16 days (mean of 4.61 days; standard deviation of 5.04 days).
579 Subjects were blinded to the stimulation order.

580 Each session consisted of a brief training period, followed by 3 formal data collection blocks of
581 208 trials, each of which lasted approximately 20 min (see Figure 2C). Training at the start of each
582 session consisted of two mini-blocks to ensure that subjects understood the task. In the first training
583 mini-block, subjects performed practice runs of 40 trials in which they counting the number of /ga/
584 syllables appearing in a 5-syllable target stream presented in quiet until they reached an accuracy
585 of 80%. In the second training mini-block, subjects performed practice runs of 48 trials identical
586 to those in the formal experimental attention task until their accuracy reached 50% (chance level
587 on this task is 17%). Subjects were allowed to repeat these training runs until they reached criteria.
588 No subjects failed to successfully meet the criteria. The majority of the subjects reached criteria
589 on each of the training tasks after only 1-2 runs; however, one subject required 8 runs of the with-
590 distractor training. The results of this subject, however, did not stand out in any way from the
591 results of the other subjects.

592 Following training in each session, subjects conducted three 20-min long blocks of 208 trials (see
593 Figure 8B). The first block served as a baseline control, with no neural stimulation. In the second
594 block, subjects received either HD-tACS stimulation or sham stimulation for 20 min. No

595 stimulation was performed in the final, third block, which allowed us to evaluate whether there
596 were any aftereffects of stimulation. Because alpha frequency stimulation has been reported to be
597 more effective in darkness⁷⁴, all subjects but one performed the experiment in the dark; the
598 exception reported suffering from claustrophobia and performed the task in typical lighting.

599 The trial order within each 208-trial block was pseudo-random, with each trial type equally likely.
600 Each block contained exactly 104 trials of *spatial* attention trials (52 attend left and 52 attend right)
601 and 104 trials of *nonspatial* attention (52 attend female and 52 attend male). Additionally, half of
602 the trials were *continuous* and the other half *switching* (e.g., each of the three blocks in an
603 experimental session contained exactly 26 trials of *attend left, continuous* trials). To avoid fatigue,
604 subjects were given a 10 s rest period after every 48 trials within each block.

605 4.4 High Definition Transcranial Alternating Current Stimulation (HD-tACS)

606 HD-tACS was administered using the Soterix M×N-9 High Definition-Transcranial Electrical
607 Current (HD-tES) Stimulator (Model 9002A, Soterix Medical, New York, NY). To target right
608 IPS, an electrode montage was created based on a current flow model generated by the Soterix
609 HD-Explore software (version 4.1, Soterix Medical, New York, NY). Stimulation electrodes were
610 placed in HD Electrode holders (Soterix Medical, New York, NY) and embedded in a 64-channel
611 EEG cap. The electrode holders were filled with gel to ensure impedance for each electrode did
612 not exceed 50 k ohms prior to stimulation and remained below 5 k ohms during stimulation⁷⁵. The
613 major stimulating electrode was placed at P2 with a stimulation intensity of 1.5mA, and 4 return
614 electrodes were placed at CP2 (-0.6mA), P4 (-0.225mA), Pz (-0.075mA), and PO4 (-0.6mA). Both
615 the HD-tACS stimulation and sham sessions used the same electrode montage. Figure 8A depicts
616 the electrode placement of the montage and simulated current-flow model.

617 Both Stimulation and Sham sessions delivered a bipolar sinusoidal waveform at 10 Hz (Figure
618 8B). Despite the fact that there are individual differences in peak frequencies of oscillation activity,
619 such as in alpha⁷⁶, we chose to stimulate at the same frequency for all subjects. When targeting
620 parietal alpha oscillations in Experiment 1, we chose a 10 Hz stimulation rate, which is close to
621 the peak reported for most subjects (in the 10-11 Hz range). Experiment 2 used a 6 Hz rate, which
622 is the median peak theta frequency.⁷⁷

623 The total current delivered was 1.5 mA at maximum. While the most effective intensity and
624 duration for HD-tACS or traditional tACS stimulation is not known, previous tACS studies have
625 commonly used 1.5 – 2 mA^{45,57,63}. With very few studies to reference on the effectiveness of HD-
626 tACS intensity, we arbitrarily chose a relatively conservative and widely used stimulation intensity
627 of 1.5 mA to mitigate any adverse effect of stimulation.⁷⁸

628 In the HD-tACS session, stimulation ramped up to 1.5 mA over 30 s at the beginning of the 20-
629 min stimulation block, and ramped down over 30 s at the end, yielding 19 min of continuous 1.5
630 mA stimulation during the middle of the block. During the middle block of the Sham session,
631 stimulation ramped up to 1.5 mA over 30 s and then immediately ramped down to 0 mA in the
632 following 30 s; in the final minute of the block, stimulation ramped up and then down. During the
633 40 s at the beginning of stimulation in both sessions, subjects were verbally checked to ensure they
634 are familiarized with the stimulation-induced sensation and that they are comfortable proceeding
635 with the experiment.

636 4.5 Statistical analysis

637 To test our hypotheses, we calculated the percentage of correct responses for each attention
638 condition (*spatial* attention: attend left vs right; *nonspatial* attention: attend female vs male). We
639 then baseline corrected for each attention condition in the during-stimulation block and post-
640 stimulation block by subtracting the accuracy of the corresponding trial type during the initial
641 baseline block. For pairwise comparisons of accuracy between conditions, due to limited number
642 of samples ($N_1=20$, $N_2=18$), a Wilcoxon signed rank test was performed (significance for $P <$
643 0.05).

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649 Data Availability

650 All data from and code used to analyze the results of this study are available online at Dryad:
651 <https://datadryad.org/review?doi=doi:10.5061/dryad.c031nv7>.⁷⁹
652

653 Competing interests

654 The authors declare no competing interests.

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