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► **To cite this version:**

Florian Kasten, Quentin Busson, Benedikt Zoefel. Opposing neural processing modes alternate rhythmically during sustained auditory attention. *Communications Biology*, 2024. hal-04250511v2

**HAL Id: hal-04250511**

**<https://hal.science/hal-04250511v2>**

Submitted on 28 Oct 2024

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1 **Opposing neural processing modes alternate rhythmically during**  
2 **sustained auditory attention**

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20 **Keywords:** brain oscillations, entrainment, auditory system, sustained attention, speech perception

21  
22 (Abstract: 191 words, Manuscript: 3929 words, Methods: 2290 words, Number of Figures: 5)

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28

29 **Abstract**

30 During continuous tasks, humans show spontaneous fluctuations in performance, putatively caused  
31 by varying attentional resources allocated to process external information. If neural resources are  
32 used to process other, presumably “internal” information, sensory input can be missed and explain  
33 an apparent dichotomy of “internal” versus “external” attention.

34 In the current study, we extract presumed neural signatures of these attentional modes in human  
35 electroencephalography (EEG): neural entrainment and  $\alpha$ -oscillations ( $\sim 10$ -Hz), linked to the pro-  
36 cessing and suppression of sensory information, respectively. We test whether they exhibit struc-  
37 tured fluctuations over time, while listeners attend to an ecologically relevant stimulus, like speech,  
38 and complete a task that requires full and continuous attention.

39 Results show an antagonistic relation between neural entrainment to speech and spontaneous  $\alpha$ -  
40 oscillations in two distinct brain networks – one specialized in the processing of external information,  
41 the other reminiscent of the dorsal attention network. These opposing neural modes undergo slow,  
42 periodic fluctuations around  $\sim 0.07$  Hz and are related to the detection of auditory targets. Our study  
43 might have tapped into a general attentional mechanism that is conserved across species and has  
44 important implications for situations in which sustained attention to sensory information is critical.

## 45 **Introduction**

46 The ability to sustain attention is crucial for many activities of everyday life, yet it is surprisingly  
47 difficult to achieve<sup>1,2</sup>. Lapses in attention are common even in healthy populations, can have negative  
48 downstream effects on cognition<sup>3</sup> and lead to human error, sometimes with major consequences<sup>4-6</sup>.  
49 A variety of neurological and psychiatric disorders are characterized or accompanied by a decreased  
50 ability to maintain sustained attention<sup>7,8</sup>. Understanding the neural processes that give rise to dy-  
51 namic fluctuations in attention is therefore critical.

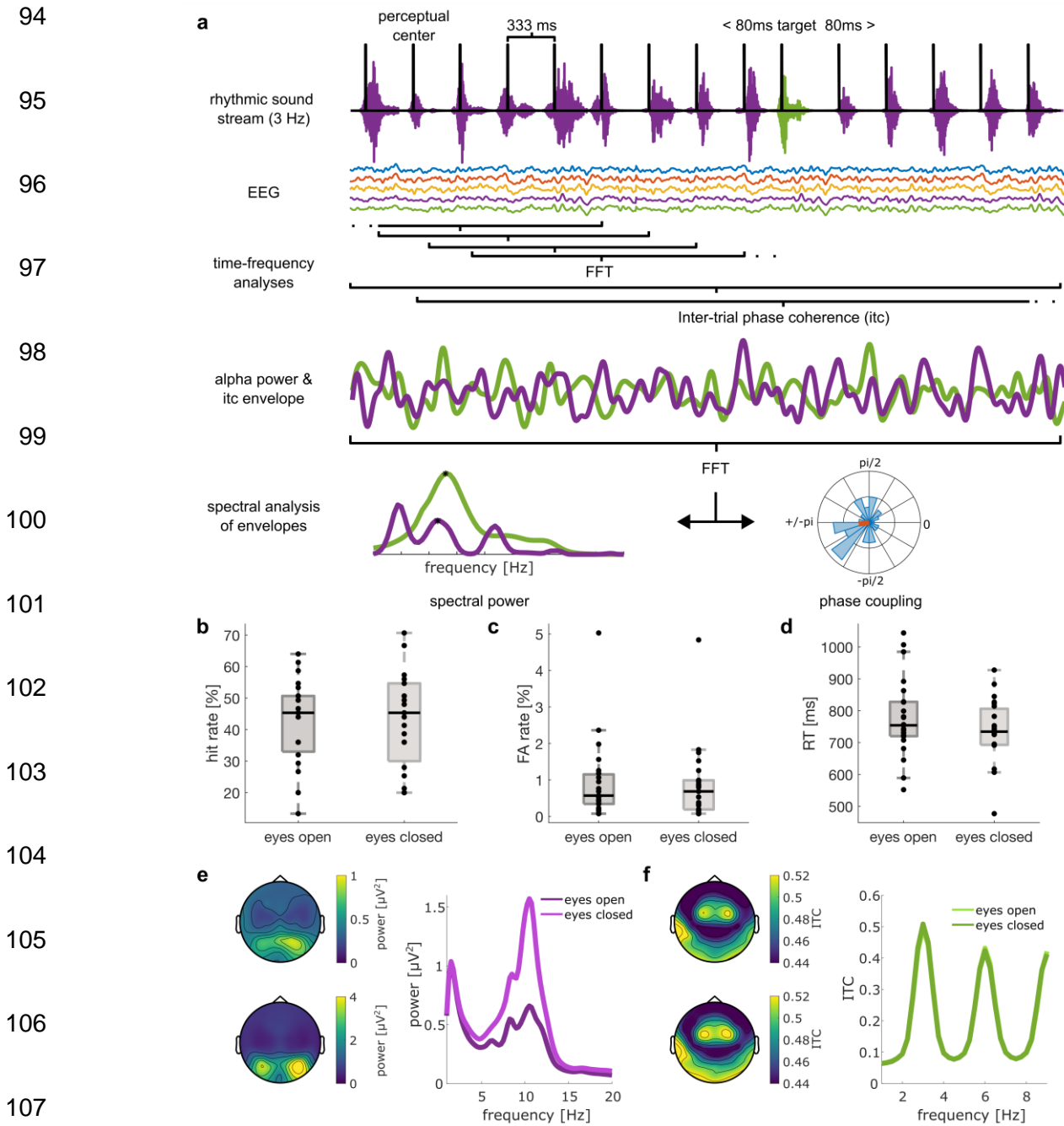
52 It has been proposed that these fluctuations arise due varying amounts of attentional resources  
53 allocated to the processing of external information. When sensory input is ignored, neural resources  
54 might be available for other processes unrelated to external information (such as memory consoli-  
55 dation or internal thought), leading to a dichotomy of “internal” versus “external” attention<sup>9,10</sup>. Each  
56 of these opposing attentional modes might have its own signature, including specific patterns of  
57 neural connectivity<sup>1,2</sup> and neural oscillations<sup>10-12</sup>. Prominently,  $\alpha$ -oscillations (~10-Hz) have been  
58 linked to suppression of sensory information<sup>13,14</sup> and attentional (de-)selection<sup>15-18</sup>, and might there-  
59 fore correspond to a state in which input is prone to be ignored. When listeners attend to rhythmic  
60 sequences, neural activity synchronizes to the stimulus rhythm, an effect often termed neural en-  
61 trainment<sup>19-21</sup>. As a potential counterpart to  $\alpha$ -oscillations, neural entrainment is therefore a prime  
62 example for a marker of active stimulus processing<sup>20,22,23</sup>. However, neural entrainment and  $\alpha$ -oscil-  
63 lations are often studied in isolation, and the few efforts to relate them<sup>24-26</sup> have used trial-based  
64 paradigms that, due to their frequent interruptions of stimulus presentation, cannot capture fluctua-  
65 tions in sustained attention.

66 One of the rare studies that did consider both of these neural markers during sustained attention  
67 measured them in the auditory cortex of macaque monkeys<sup>10</sup>. This work supported the notion that  
68 internal attention is characterized by strong  $\alpha$ -oscillations and reduced sensitivity to external infor-  
69 mation<sup>10</sup>. When subjects listened to rhythmic tone sequences, neural activity synchronized to the  
70 stimulus rhythm<sup>19,25,26</sup>. At certain times, however, neural entrainment was reduced and  $\alpha$ -oscillations  
71 dominated processing in auditory cortex. When  $\alpha$ -oscillations prevailed, they rhythmically modulated  
72 neuronal firing and reduced neural and behavioral responses to stimulus input. Fundamental for our

73 study, these bouts of  $\alpha$ -oscillations (i.e. internal attention) occurred regularly and alternated with  
74 periods of strong entrainment to sound (i.e. external attention), at an inherent rhythm of  $\sim 0.06$  Hz  
75 (i.e.,  $\sim 16$ -sec)<sup>10</sup>.

76 The identification of rhythmicity in attentional states and their neural counterparts has important im-  
77 plications for future research. It could be leveraged in the design of critical systems technology,  
78 educational environments or in the design of interventional approaches for situations where sus-  
79 tained attention is critical. However, it remained elusive if humans possess equivalent neural signa-  
80 tures of attentional modes, and whether they exhibit any temporal regularity. It also remained unclear  
81 if regular attentional lapses occur during the processing of ecologically relevant stimuli. Human  
82 speech requires integration of information over time to be optimally perceived<sup>27</sup>. It therefore needs  
83 full and continuous attention, and regular attentional lapses seem particularly harmful for speech  
84 processing. Finally, the network structure governing the hypothesized modes in auditory sustained  
85 attention remained unaddressed thus far.

86 In the current study, we recorded electroencephalographic (EEG) data in humans and tested for  
87 regular fluctuations in attentional modes while participants paid sustained attention to rhythmic  
88 speech sounds. We hypothesized that, similar to the aforementioned findings in non-human pri-  
89 mates<sup>10</sup>, neural entrainment to speech and spontaneous  $\alpha$ -oscillations show rhythmic fluctuations at  
90 ultra-slow frequencies close to  $\sim 0.06$  Hz (0.02-Hz - 0.2-Hz) and that these fluctuations show an  
91 antagonistic relationship (i.e. are coupled in anti-phase). Given its strong environmental rhythms<sup>28</sup>,  
92 we here chose to focus on the auditory modality. However, our findings may pave the way for inves-  
93 tigations into rhythmic attentional fluctuations across sensory modalities.



108 **Figure 1: Experimental design & analysis.**

109 **(a)** Participants listened to continuous 5-min streams of rhythmic, monosyllabic French words pre-  
 110 sented at a rate of 3-Hz (top). Spectral analysis was performed on 2-s EEG segments centered on  
 111 the perceptual center of each word. 15 adjacent segments (~5-sec window) were integrated in a  
 112 sliding window approach to compute inter-trial coherence (ITC) over time. ITC at 3-Hz and power in  
 113 the  $\alpha$ -band (8 – 12-Hz) were extracted and treated as new time-series (4<sup>th</sup> row). The two time-series  
 114 were submitted to another spectral analysis to assess slow, rhythmic fluctuations of  $\alpha$ -oscillations  
 115 and auditory entrainment. We identified prominent spectral peaks in both spectra and assessed their  
 116 coupling and phasic relation (bottom row). **(b+c)** Proportion of hits and false alarms in eyes-open  
 117 and eyes-closed conditions. **(d)** Reaction times for hits. **(e)** Topography of  $\alpha$ -power in eyes-open  
 118 (top) and eyes-closed (bottom) conditions. Spectra on the right have been extracted from channel  
 119 Pz and averaged across subjects. **(f)** Same as e, but for ITC (spectra are shown for channel Fz).  
 120 Both  $\alpha$ -power and ITC spectra and topographies are consistent with previous reports in the literature.  
 121 Boxplots depict the median of the data  $\pm$  interquartile range. Whiskers indicate the range of the data.

122 **Results**123 **Overview**

124 We recorded EEG from  $n=23$  participants while they listened to 5-min streams of rhythmic, mono-  
125 syllabic, French words presented at a rate of 3-Hz (**Fig. 1a**). Depending on the experimental block,  
126 participants were instructed to keep their eyes open or closed, respectively. They were asked to  
127 identify words that were presented off-rhythm (i.e., shifted by 80-ms relative to the 3-Hz rhythm). On  
128 average, participants detected 41.22% ( $\pm$  *SD*: 13.80) of targets during the eyes-open and 42.96% ( $\pm$   
129 *SD*: 15.56) during eyes-closed (**Fig. 1b**) conditions. The proportion of false alarms was low relative  
130 to the large number of non-target words (eyes-open: 0.91%  $\pm$  *SD*: 1.06, eyes-closed: 0.83%  $\pm$  *SD*:  
131 1.00, **Fig. 1c**). There was no difference in hits or false alarms between eyes-closed and eyes-open  
132 conditions (dependent samples t-test, hits:  $t_{22} = -0.94$ ,  $p = .35$ , FA:  $t_{22} = 1.11$   $p = .27$ ), nor was there  
133 a difference in reaction times ( $t_{22} = 1.62$ ,  $p = .12$ :  $M_{eyes-open} = 777$ -ms  $\pm$  *SD*: 122;  $M_{eyes-closed} = 738$ -ms  
134  $\pm$  *SD*: 96, **Fig. 1d**).

135 We used standard spectral analysis methods to extract spontaneous  $\alpha$ -oscillations, and inter-trial  
136 coherence (ITC)<sup>10,23</sup> at 3-Hz to quantify auditory entrainment (see Materials and Methods). Both  
137 showed EEG topographies consistent with the literature<sup>23,29</sup> (**Fig 1e,f**).  $\alpha$ -oscillations showed a dom-  
138 inant occipito-parietal topography with a prominent increase in power when participants closed their  
139 eyes<sup>29</sup> (**Fig. 1e**). Auditory entrainment was dominant in fronto-central sensors with peaks in the ITC  
140 spectrum at the 3-Hz stimulus rate and its harmonic frequencies<sup>19,23,30</sup> (**Fig. 1f**).

141

142  **$\alpha$ -oscillations and entrainment show slow fluctuations at similar time scales**

143 Adapting an approach from Lakatos et al.<sup>10</sup> to human EEG, we traced the evolution of spontaneous  
144  $\alpha$ -power and auditory entrainment during the task (**Fig. 1a**). We used a sliding window approach to  
145 quantify how both of these measures change over time (see Materials and Methods).

146 We found that both  $\alpha$ -oscillations and neural entrainment exhibit slow, regular fluctuations (**Fig. 2 a**).  
147 The dominant frequency in these fluctuations, which we revealed as 0.07-Hz ( $\sim$ 14 sec,  $M_{\alpha} =$   
148 0.0713-Hz  $\pm$  *SD* = 0.0126,  $M_{ITC} = 0.0710$ -Hz  $\pm$  *SD* = 0.0116), was strikingly similar to that reported

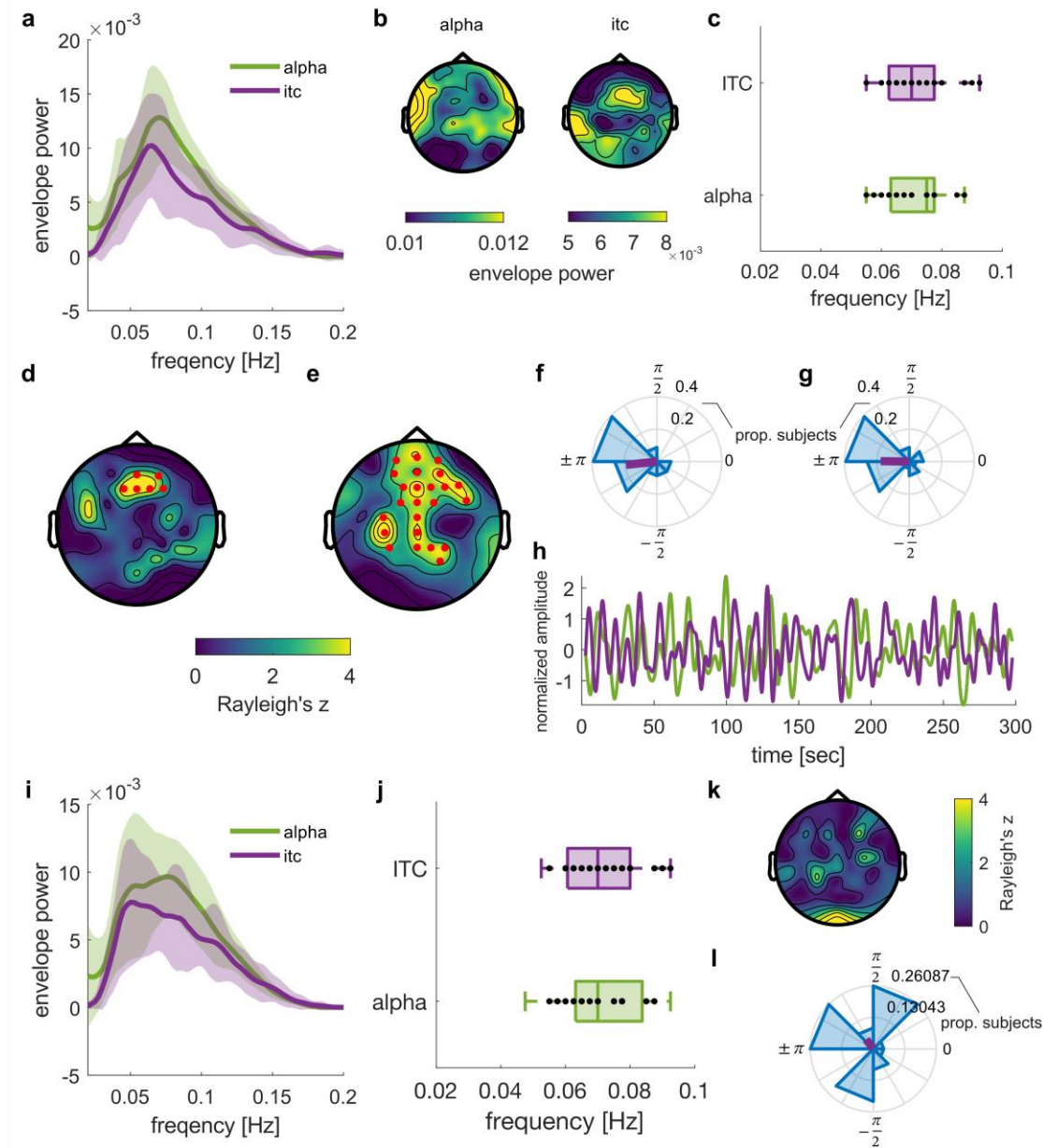
149 in non-human primates<sup>10</sup>. While the topographical distribution of entrainment fluctuations (**Fig. 2b**)  
150 resembled that of entrainment itself (**Fig. 1e**), this was not the case for  $\alpha$ -oscillations. This result  
151 implies that the observed fluctuations in  $\alpha$ -power (**Fig. 2b**) might be indeed linked to auditory atten-  
152 tional processing, in contrast to the distribution of  $\alpha$ -power that is generally dominated by the visual  
153 system (**Fig. 1d**).

154  $\alpha$ -oscillations and entrainment did not only fluctuate at similar time scales on the group level (**Fig.**  
155 **2c**), but also within individuals: On average, the individual peak frequency for  $\alpha$ -power fluctuations  
156 did not differ from that for neural entrainment (dependent samples t-test:  $t_{22} = 0.08$ ,  $p = .93$ ;  $M_{|alpha -$   
157  $|TCI|} = 0.015\text{-Hz} \pm SD = 0.0112\text{-Hz}$ ). Together, we found that  $\alpha$ -oscillations and neural entrainment  
158 exhibit similar slow, regular fluctuations.

### 159 **Anti-phasic relation between $\alpha$ -power and entrainment fluctuations**

160 We next assessed if the rhythmic fluctuations of  $\alpha$ -oscillations and auditory entrainment are coupled.  
161 If the two reflected opposing processing modes, they should show an anti-phase relationship: When  
162  $\alpha$ -oscillations are strong, neural entrainment should be reduced, and vice versa. To this end, we  
163 computed the average phase difference between  $\alpha$ -power and entrainment fluctuations for each  
164 EEG channel. Our analysis revealed a significant coupling (i.e., consistent phase relation) between  
165  $\alpha$ -power and entrainment across subjects within a cluster of fronto-central channels (cluster-based  
166 Rayleigh's test;  $p_{cluster} = .037$ , **Fig. 2d**, see **Supplementary Table 1** for an overview of channels  
167 within the cluster). A circular one-sample test yielded a significant deviation of the average phase  
168 difference from zero ( $p < .001$ ). This average phase difference was close to anti-phase ( $M_{angle} = -$   
169  $3.04$  rad), and with the 99% confidence interval for the sample mean including  $\pm \pi$  ( $CI_{99} = 2.39, -$   
170  $2.18$ , **Fig. 2f**). **Supplementary Fig. S1a** provides an overview of the phase distribution in each EEG  
171 channel. Importantly, the anti-phasic relation of the two signals was evident on single subject level.  
172 14 out of 23 participants show a significant coupling within the identified cluster. For 15 out of 23  
173 participants, the average angle between  $\alpha$ -power and entrainment fluctuations significantly differed  
174 from 0 (**Supplementary Fig. S1b**). We could not identify reliable differences in oscillatory features  
175 or other variables that can distinguish these 15 participants from the others (**Supplementary Fig.**  
176 **S2, Supplementary Note 1**).





177

178

179 **Figure 2:  $\alpha$ -power and entrainment exhibit slow anti-phase fluctuations.**

180 **(a-h)** Results for eyes-open condition. **(a)** Envelope spectra of  $\alpha$ -power and entrainment to rhythmic  
 181 speech show a peak around 0.07-Hz (shown for electrode Fz). **(b)** Topography of the 0.07-Hz peak  
 182 shown in a. **(c)** Distribution of individual peak frequencies from the spectra shown in a. **(d)** Coupling  
 183 between  $\alpha$ -power and entrainment fluctuations around 0.07-Hz when both were extracted from the  
 184 same channel. Channels showing a significant non-uniform distribution of phase differences are  
 185 highlighted in red, topography indicates the underlying z-statistic. **(e)** Channels showing significant  
 186 coupling between  $\alpha$ -power fluctuations per channel with entrainment in the frontal cluster (d). **(f)**  
 187 Distributions of phases in channels showing significant  $\alpha$ -power vs. entrainment coupling (cluster  
 188 shown in d).  $\alpha$ -power and entrainment to speech are coupled in anti-phase. **(g)**  $\alpha$ -power fluctuations  
 189 in cluster shown in (e) are coupled in anti-phase. **(h)** Exemplary time-course of  $\alpha$ -power and entrain-  
 190 ment fluctuations at electrode Fz. **(i-l)** same as a, c, d, g, but for eyes-closed condition. Shaded  
 191 areas depict standard deviation. Boxplots depict the median of the data  $\pm$  interquartile range. Whisk-  
 192 ers indicate the range of the data.

193

194 For results described above and shown in **Fig. 2d**, we contrasted  $\alpha$ -power and entrainment from the  
195 same EEG channels. We next tested whether different channel combinations produce similar results.  
196 The topographical distribution of auditory entrainment in the EEG is well established and was repro-  
197 duced in our results (**Figs. 2b,d**). However,  $\alpha$ -oscillations are typically dominated by vision and their  
198 topographical pattern was more difficult to predict in our case. We therefore assessed, separately  
199 for each channel, whether  $\alpha$ -power in this channel is coupled with neural entrainment in the frontal  
200 channel cluster shown in **Fig. 2d**. The analysis revealed a more distributed cluster of fronto-central  
201 and parietal channels in which  $\alpha$ -power fluctuations are coupled to auditory entrainment (random  
202 permutation cluster Rayleigh-test:  $p_{cluster} = .042$ , **Fig. 2e**, see **Supplementary Table 1** for an over-  
203 view of channels within the cluster). Again, the difference between entrainment and  $\alpha$ -power fluctu-  
204 ations was close to anti-phase within this cluster ( $M_{angle} = 3.13$  rad, circular one-sample test against  
205 angle of zero:  $p < .01$ ) with the 99% CI for the sample mean including  $\pm \pi$  ( $CI_{99} = 2.16, -2.18$ , **Fig.**  
206 **2g**). **Fig. 2h** depicts an exemplary time course of  $\alpha$ -power and entrainment fluctuations. An example  
207 for each participant is shown in **Supplementary Fig. S1c**. In control analyses, we ruled out that the  
208 fluctuations observed in the  $\alpha$ -band are driven by harmonic entrainment at frequencies in the  $\alpha$ -band  
209 (**Supplementary Fig. S3**). Together, we found an anti-phase relation between the slow fluctuations  
210 in  $\alpha$ -power and neural entrainment, as predicted from two opposing neural processes<sup>9,12</sup>.

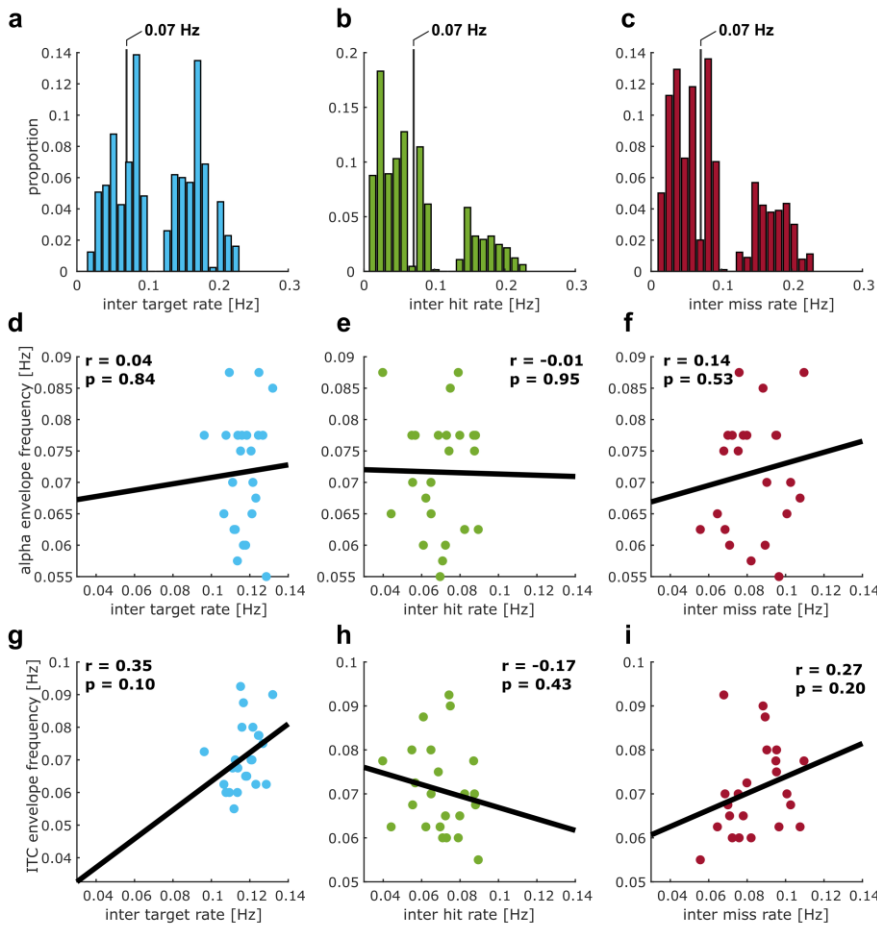
### 211 **Anti-phase relation between entrainment and $\alpha$ -oscillations is state dependent**

212 When participants were instructed to close their eyes during the task, the 0.07-Hz peaks became  
213 less pronounced, compared to the eyes-open condition (**Fig. 2i-l**). Further, we did not find evidence  
214 for a significant coupling ( $p_{cluster} > .68$ , **Fig. 2k**) nor anti-phase relationship (circular one-sample test  
215 against angle of zero:  $p > .05$ ,  $M_{angle} = 2.22$  rad, **Fig. 2l**) between  $\alpha$ -oscillations and entrainment  
216 when the eyes were closed.

### 217 **Slow rhythmic fluctuations cannot be explained by stimulus properties**

218 Although time intervals between targets were selected from a wide range and therefore irregular,  
219 their average (25 targets in 300 seconds) resembled the period of the slow neural fluctuations re-  
220 ported. To rule out that some regularity in target presentation explains the slow rhythmicity in  $\alpha$ -

221 power or auditory entrainment, we computed the distribution of time intervals between targets (Fig.  
 222 3a), hits (Fig. 3b), and misses (Fig. 3c). None of these distributions shows a bias for 14 s (which  
 223 would correspond to the 0.07 Hz rhythm found in  $\alpha$ -power and ITC). Moreover, we found that indi-  
 224 vidual frequencies for slow changes in  $\alpha$ -power and ITC are uncorrelated with corresponding inter-  
 225 vals between targets (Fig. 3d,g), hits (Fig. 3e,h), or misses (Fig. 3f,i). It therefore seems unlikely that  
 226 the rate of target presentation gave rise to the observed fluctuations in the EEG.



227

### 228 **Figure 3: Control analysis.**

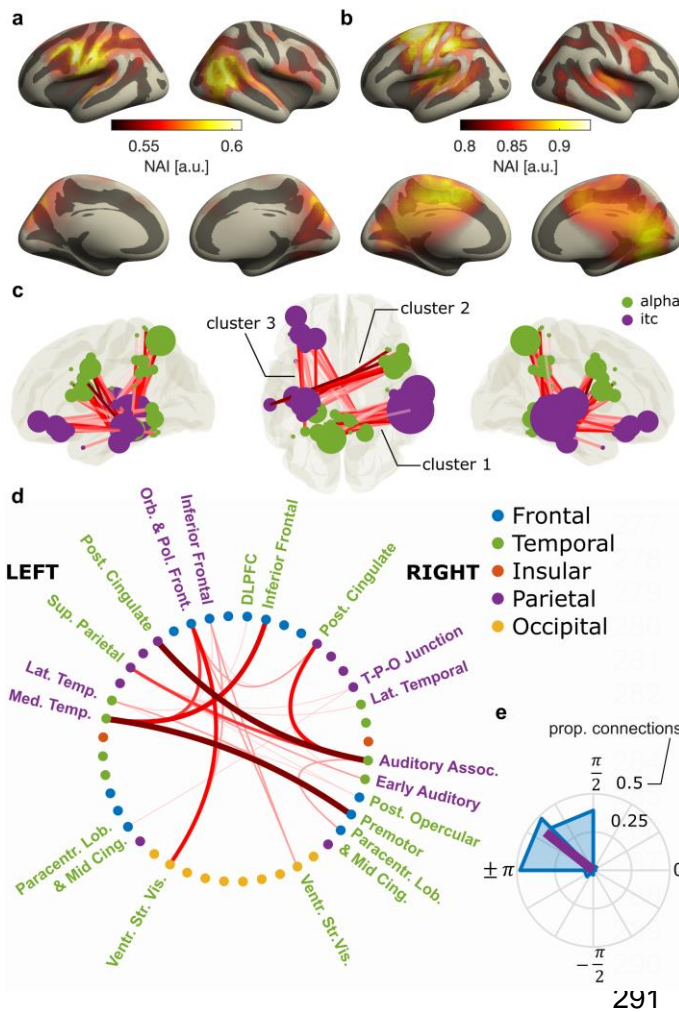
229 (a-c) Distribution of time intervals between targets (a), hits (b), and misses (c), pooled across sub-  
 230 jects for the eyes-open condition. Intervals were converted to rate (in Hz) for comparability with neu-  
 231 ral fluctuations. Vertical line indicates 0.07 Hz. (d-i) Correlations between individual frequencies for  
 232 slow fluctuations in alpha power (middle row) or ITC (bottom row) and average intervals between  
 233 targets (d,g), hits (e,h), or misses (f,i) while these fluctuations were measured.

234

**235 Opposing attentional modes emerge from interactions of distinct cortical networks**

236 To reveal the neural sources of opposing attentional modes, we source localized the slow rhythmic  
237 fluctuations in neural entrainment (**Fig. 4a**) and  $\alpha$ -power (**Fig. 4b**) in the eyes-open condition, using  
238 a frequency domain beamformer<sup>31</sup> at the individual peak frequency of  $\alpha$ -power fluctuations used in  
239 the previous analyses (**Fig. 2c**). For both of these, we observed activity in regions associated with  
240 auditory and speech processing including Superior Temporal Gyrus (STG), as well as left Pre-Cen-  
241 tral Gyrus. For entrainment (**Fig. 4a**), we found an additional involvement of left Inferior Frontal Gyrus  
242 (IFG) as well as the right Inferior Parietal Lobe, Angular Gyrus and parts of posterior STG. For  $\alpha$ -  
243 power (**Fig. 4b**), we found additional activity in left Post-Central Gyrus, Superior Parietal Lobe as  
244 well as Posterior Cingulate and Occipital Cortex.

245 We then quantified coupling between neural entrainment and  $\alpha$ -power as a phase relation between  
246 the two that is consistent across participants. This approach was similar to the previous sensor-level  
247 analysis, only that is was applied to different combinations of 360 cortical regions-of-interest (ROIs),  
248 parcellated on the source level according to the HCP-MMP1 atlas of the human connectome pro-  
249 ject<sup>32</sup>. We found significant coupling between slow entrainment changes bilaterally in ROIs in tem-  
250 poral cortex and left Inferior Frontal Gyrus, and equivalent changes in  $\alpha$ -power in bilateral Posterior  
251 Cingulate Cortex, Superior Parietal Lobe and right Inferior Frontal Gyrus (permutation cluster Ray-  
252 leigh-test with three significant clusters:  $p_{\text{cluster1}} = .0026$ ,  $p_{\text{cluster2}} = .004$ ,  $p_{\text{cluster3}} = .006$ ; **Fig. 4c**). **Table**  
253 **1** provides an overview of ROIs within the significant clusters, **Fig. 4d** depicts coupling for ROIs  
254 sorted into 44 higher order cortical structures according to the HCP-MMP1 atlas. Again, the coupling  
255 was driven by a phase relation between ROIs that was close to anti-phase (**Fig. 4e**). Whereas  
256 structures showing coupled fluctuations in entrainment are typically associated with processing of  
257 speech<sup>33–36</sup> (and therefore may reflect attention to sensory input), those with corresponding  $\alpha$ -fluc-  
258 tuations involve regions associated with fronto-parietal attention networks<sup>37,38</sup>, but also the default  
259 mode network<sup>38,39</sup>. Together, these results imply that fluctuations in opposing attentional modes may  
260 stem from an interaction between distinct cortical networks, one associated with active processing  
261 of external stimuli (i.e., the speech network), and the other concerned with up- and down-regulation  
262 of processing resources via inhibitory  $\alpha$ -oscillations.



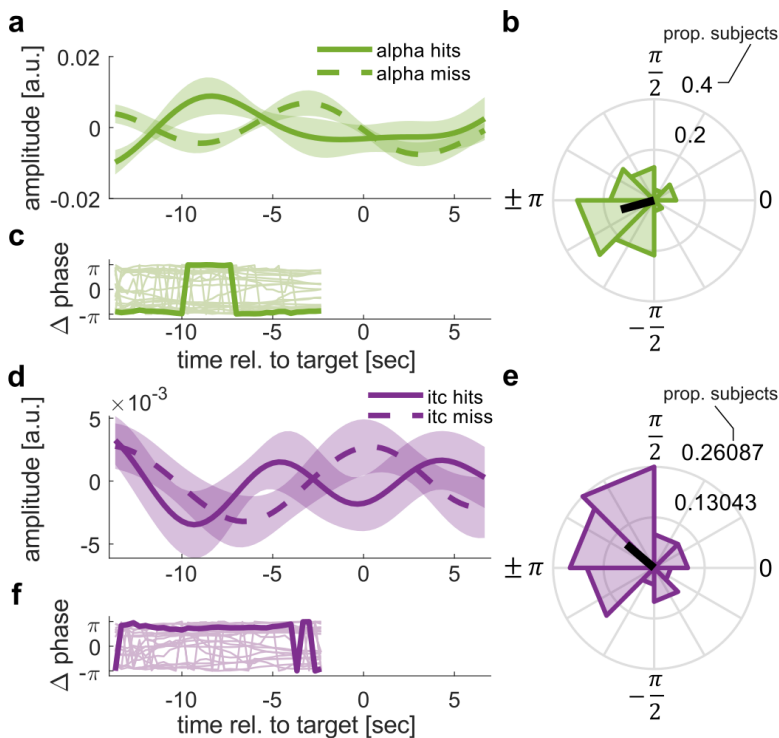
**Figure 4: Source-level analyses of  $\alpha$ -power and entrainment fluctuations.**

(a & b) Neural activity index (NAI) of rhythmic fluctuations in entrainment (a) and  $\alpha$ -power (b). (c) Coupling between  $\alpha$ -power and entrainment fluctuations across 360 cortical ROIs. Each circle indicates the location of an ROI that belongs to a cluster with significant coupling. The size of the circle indicates the number of ROIs significantly coupled to each ROI. Lines indicate coupling between an ROI's entrainment fluctuations and another ROI's  $\alpha$ -power fluctuations. Darker shades of red indicate stronger coupling. We found three clusters with significant coupling – 1: parietal ( $\alpha$ ) to right temporal (entrainment), 2: right frontal ( $\alpha$ ) to left temporal (entrainment), 3: parietal ( $\alpha$ ) to left frontal(entrainment) (d) Overview of cortical structures, extracted from the HCP-MMP1 atlas, that contain ROIs with coupling between  $\alpha$ -power and entrainment fluctuations. Thicker, darker lines indicate more connections between ROIs in two given structures. Font color indicates if a structure shows (predominantly) entrainment (violet) or  $\alpha$ -power coupling. (e) Distribution of phase differences between  $\alpha$ -power and entrainment fluctuations from all ROIs that are part of the significant clusters.

## 292 Neural signatures of attentional mode differ between detected and missed target stimuli

293 Thus far we have reported a systematic coupling between slow fluctuations of  $\alpha$ -power and auditory  
 294 entrainment to rhythmic speech. Periods of stronger entrainment and lower  $\alpha$ -power alternated with  
 295 periods of weaker entrainment and higher  $\alpha$ -power. If such periods are indeed indicative of different  
 296 attentional processing modes, they should also be related to target detection. In other words,  $\alpha$ -  
 297 power (or entrainment) fluctuations prior to detected targets should be in opposite phase as com-  
 298 pared to missed ones. **Fig. 5a,c** depicts the average time courses of  $\alpha$ -power and entrainment fluc-  
 299 tuations around hits and misses (bandpass filtered around the individual peak frequencies around  
 300 0.07-Hz). We computed the instantaneous phase of these time courses on an individual level. We  
 301 observed a systematic clustering of phase differences between hits and misses for both  $\alpha$ -power  
 302 (Rayleigh test:  $p = 0.009$ ,  $z = 4.61$ ), and entrainment fluctuations (Rayleigh test:  $p = .049$ ,  $z = 2.07$ )  
 303 in the time period before a target occurred (-14-sec to -2.5-sec). Importantly, the mean angle of this  
 304 difference significantly differed from 0 (circular one-sample test against angle of zero; alpha:  $p <$

305 0.01,  $M_{angle} = -2.87$ ,  $CI_{99} = 2.42, -1.88$ ; entrainment:  $p < 0.05$ ,  $M_{angle} = 2.44$  rad,  $CI_{95} = 1.52, -2.93$ ).  
 306 The  $CI_{99}$  of this difference included  $\pm \pi$  (**Fig. 5b,e**), indicating an anti-phase relation. The observed  
 307 phase relations appeared to be relatively stable across the pre-stimulus time period (**Fig. 5c,f**). To-  
 308 gether, we found that the hypothesized markers of attentional processing (entrainment vs.  $\alpha$ -power)  
 309 differ depending on whether an auditory target was detected or not, as expected from modes of  
 310 external and internal attention, respectively.



**Figure 5:  $\alpha$ -power and entrainment fluctuations differ between detected and missed targets.**

(a) Average, bandpass filtered  $\alpha$ -power fluctuations around hits and misses extracted from significant cluster shown in Fig. 2e. Note that data after -2.5 s can be affected by “smearing” of post-target data and thus cannot be interpreted in light of our hypothesis. (b) Polar histogram depicts the distribution of phase differences between  $\alpha$ -power fluctuations prior to hits and misses, respectively (-14-sec to -2.5-sec). (c) Event-related phase difference of  $\alpha$ -power fluctuations prior to hits and misses. Thin lines indicate single subject time-courses. Bold line depicts the circular average. Data is only shown for the time period used for statistical analysis. Note that  $-\pi = \pi$ , suggesting a stable phase opposition

333 between envelopes preceding hits and misses, respectively. (d-f) Same as a-c, but for ITC. Shaded  
 334 areas indicate standard error of the mean.

## 335 Discussion

336 Variations in performance are a prominent feature of sustained attention. In the current study, our  
 337 marker of sustained attention to speech – neural entrainment – exhibited slow fluctuations with an  
 338 inherently rhythmic component (**Fig. 2a**). Importantly, these fluctuations were opposite to those in  $\alpha$ -  
 339 oscillations (**Fig. 2f**), commonly assumed to reflect suppressed sensory input<sup>13,14</sup> and therefore in-  
 340 dicative of an opposite mode of “internal” attention. In addition, neural signatures of attentional mode  
 341 differed depending on whether a target was detected or not (**Fig. 5**). Our results therefore demon-  
 342 strate that lapses in (external) attention occur rhythmically, even when presented with a stimulus that  
 343 requires sustained attention for successful comprehension. Moreover, these fluctuations occurred at

344 time scales (~14-sec) that are very similar to those observed in non-human primates<sup>10</sup>. Thus, we  
345 might have tapped into a general property of sustained attention that is conserved across species.  
346 The questions whether attention to sensory input always includes regular lapses, and which experi-  
347 mental manipulations can make attention more “sustained” need to be addressed in future work.  
348 Our results indicate that fluctuations in attentional modes may emerge from interactions of distinct  
349 brain networks. Defined as neural activity aligned to a stimulus rhythm<sup>19,20,22</sup>, we here used neural  
350 entrainment as a marker for sensory processing, and therefore external attention. We used rhythmic  
351 speech as the entraining stimulus, given its role in human communication and ability to entrain en-  
352 dogenous brain oscillations<sup>19,20,22,23,40</sup>. In line with this approach, the network exhibiting slow, rhyth-  
353 mic fluctuations in entrainment entailed auditory and inferior frontal regions that typically entrain to  
354 auditory stimuli and speech in particular<sup>40,41</sup>, and are involved in phonological and semantic pro-  
355 cessing<sup>42</sup>.

356 Our results imply that, in moments with reduced external attention and corresponding decrease in  
357 neural entrainment,  $\alpha$ -power increases in a network including Superior Parietal Lobe, Posterior Cin-  
358 gulate Cortex, and right IFG. Many of these regions have been associated with dorsal (and ventral)  
359 fronto-parietal attention networks<sup>37,38,43</sup>. These networks have previously been suggested to support  
360 attention in different modalities, although the exact regions involved may not overlap completely<sup>44,45</sup>.  
361 However, they have been predominantly studied in vision and evidence for their involvement in au-  
362 ditory, and particularly in sustained attention is scarce. Parts of Posterior Cingulate Cortex are also  
363 implicated in the default mode network<sup>39</sup>. Activity in this network has been associated with internal  
364 attention and reduced processing of external stimuli, resulting in attentional lapses<sup>1,2</sup>. Importantly,  
365 attention and default mode networks are typically localized with functional magnetic resonance im-  
366 aging (fMRI), which offers high spatial resolution, but cannot resolve the role of brain oscillations in  
367 the regions. In contrast, previous research has linked  $\alpha$ -oscillations to inhibition of sensory pro-  
368 cessing<sup>13,14,46,47</sup> and attentional (de-)selection<sup>15–18,48</sup>. In the context of sustained attention, high levels  
369 of  $\alpha$ -oscillations are associated with attentional lapses<sup>10,11,49</sup> and periods of mind wandering<sup>50</sup>. How-  
370 ever, these fields of research mostly exist in isolation, and it remained unclear to what extent brain  
371 networks found in fMRI and those that give rise to  $\alpha$ -oscillation effects in attention overlap. Although

372 causality needs to be tested in follow-up work, our results suggest that dorsal attention and default  
373 mode networks may exercise rhythmic top-down control of sensory processing via  $\alpha$ -oscillations,  
374 leading to slow, regular changes between internal and external attention.

375 While previous research has investigated the role of  $\alpha$ -oscillations and neural entrainment to speech,  
376 only few works have considered them in conjunction<sup>24-26</sup>. Although two of these studies indicate  
377 some link between  $\alpha$ -oscillations and neural entrainment<sup>24,26</sup>, other work suggested that they are  
378 independent measures of neural activity<sup>25</sup>, in apparent conflict with the current findings. However,  
379 most of this earlier work focused on fluctuations in  $\alpha$ -power lateralization over time and consequently,  
380 on spatial rather than sustained attention. The “lateralization index” employed in these studies might  
381 have removed slow fluctuations in  $\alpha$ -power that occur during sustained attention. Moreover, the trial-  
382 based experimental design used is - due to frequent interruptions or changes in stimulus presenta-  
383 tion – likely inadequate to capture slow changes in attention that we hypothesized to occur during  
384 repetitive sensory stimulation. Accordingly, the constant 3-Hz rhythm in our experimental design  
385 might have been crucial to discover the slow anti-phasic fluctuations reported here. Indeed, research  
386 in the visual domain that did employ continuous reaction tasks<sup>11,46,47</sup> used  $\alpha$ -power to predict lapses  
387 in attention up to 20 seconds before they occur. Interestingly, although not explored by the authors,  
388  $\alpha$ -power time courses seemed to contain a slow rhythmic component similar to the one observed  
389 here (cf. Fig. 5 in Ref<sup>11</sup>). Nevertheless, the fact that  $\alpha$ -oscillations and neural entrainment fluctuate  
390 in slow anti-synchrony during sustained attention but not necessarily on a shorter time scale is an  
391 interesting observation that deserves closer examination.

392 It remains unclear why the observed effects vanish when participants close their eyes. Closing the  
393 eyes is known to cause a substantial increase of  $\alpha$ -oscillations pre-dominantly in visual areas<sup>29</sup>. It is  
394 possible that these enhanced visual  $\alpha$ -oscillations overshadow their auditory and parietal counter-  
395 parts when eyes are closed, such that their coupling to auditory entrainment cannot be traced any-  
396 more. Alternatively, eye-closure may cause a fundamental change in the brain’s processing mode.  
397 Blocking visual input may allow to allocate more cognitive resources to auditory processing, such  
398 that rhythmic switching may occur at fundamentally different frequencies or is not necessary at all.



399 Our results pose important questions about the putative mechanisms driving the remarkable rhythmicity of attentional fluctuations observed in our data and their function. An obvious concern might be that the rhythmicity is inherently driven by the regularity of the stimulus material. However, this seems unlikely. Low frequency effects caused by the rhythmicity of the stimulus material should follow the principles of synchronization theory, which would predict such effects to occur at precise, predictable subharmonic frequencies<sup>51</sup>, while the fluctuations we observe in our data vary across participants. In a control analysis, we did not find any relationship between the rate of targets and the frequency of slow  $\alpha$ -power and ITC fluctuations (**Fig. 3**).

407 It therefore seems likely that the observed fluctuations are intrinsically driven. Indeed, at the level of short sub-second time-scales it has been repeatedly suggested that perceptual and attentional sampling are inherently rhythmic, fluctuating in the range of theta and  $\alpha$ -oscillations<sup>52-59</sup>. It may thus be plausible that rhythmicity in attention can also exist at other time scales. We speculate that regular changes between internal and external attention reflect a protective mechanism to prevent depletion of attentional resources. Fluctuations in attention may allow the system to maintain a higher-level of performance for a longer period of time at the cost of regular periods of reduced sensory processing. Indeed, evidence from non-invasive brain stimulation suggests that enhancing endogenous  $\alpha$ -oscillations with electrical stimulation has a stabilizing, rather than a decremental effect on sustained attention<sup>60</sup>.

417 There is an intriguing similarity of timescales between the intrinsic attentional rhythms in our data and the known coupling between  $\alpha$ -oscillations and slow rhythmic activity in the respiratory system<sup>61</sup>, the heart, and the gut<sup>62</sup>. In particular, the gastric network seems to generate rhythmic activity at similar time scales as those we found here ( $\sim 0.05$  Hz)<sup>62,63</sup>, and modulate the amplitude of spontaneous  $\alpha$ -oscillations<sup>64</sup>. Future research should address if these similarities in time scales are functionally meaningful. A recent magnetoencephalography (MEG) study supports this notion as it localized gastric- $\alpha$  coupling to right IFG and parietal lobe<sup>64</sup>, regions that overlap with the attention-related networks reported in our study.

425 A systematic rhythmicity of attentional fluctuations has important implications for both basic and applied research. Considering rhythmicity may make attentional lapses more predictable and offer a

427 potential target for interventional approaches. For example, transcranial alternating current stimula-  
428 tion (tACS) can be used to modulate brain oscillations<sup>65-67</sup> and has been previously shown to stabi-  
429 lize sustained attention when applied in a continuous manner<sup>60</sup>. Considering fluctuations of atten-  
430 tional modes may allow to apply tACS in a state-dependent manner, e.g., to induce shifts in the  
431 attentional state by applying stimulation either in the  $\alpha$ -frequency range or in synchrony with the  
432 external stimulus. Such targeted intervention may offer novel opportunities to improve or steer sus-  
433 tained attention performance in critical systems or in neurological or psychiatric patients suffering  
434 from deficits in sustained attention<sup>7,8</sup>. Our source-localization results reveal regions that can be tar-  
435 geted to modulate attentional modes. Before moving to such practical applications, additional re-  
436 search should investigate to what extent the current findings generalize across sensory systems.  
437 Compared to other sensory domains with a more static input, audition is special in that information  
438 is inherently transient and may thus benefit more from processing principles that take its temporal  
439 structure into account<sup>68</sup>. It thus remains to be determined if similar rhythmicity exists when sustained  
440 attention is deployed to visual, somatosensory, or cross-modal tasks and if so, at which frequencies  
441 rhythmicity emerges, and whether the same attentional networks engage in its regulation. First evi-  
442 dence for similar effects in the visual domain has already been reported in non-human primates<sup>10</sup>

## 443 **Materials & Methods**

### 444 **Participants**

445 Twenty-three healthy volunteers (age 22.4 years  $\pm$  1.6 years, 15 females) participated in the study.  
446 They gave written informed consent prior to joining the experiment and were paid for their participa-  
447 tion. The study was approved by the ethics board CPP (Comité de Protection des Personnes) Ouest  
448 II Angers (protocol no: CPP 21.01.22.71950 / 2021-A00131-40). All ethical regulations relevant to  
449 human research participants were followed.

### 450 **Experimental Design**

451 Over the course of six 5-min blocks, participants were instructed to listen to continuous streams of  
452 rhythmic, one-syllable French words and to indicate if they detected deviations from the rhythm via  
453 a button press on a standard computer keyboard. In the beginning of each block, they were instructed  
454 to either keep their eyes-open and fixated on a white cross at the center of a computer screen, or to  
455 keep them closed. Half the blocks were assigned to the eyes-open, and eyes-closed conditions re-  
456 spectively. The order of blocks was randomized to avoid time-on task effects. Participants were fa-  
457 miliarized with the task prior to the main experiment. They were shown examples of continuous  
458 rhythmic speech trains as well as streams containing violations of the rhythm. Subsequently, they  
459 performed a 1-min practice run of the task.

### 460 **Apparatus and stimuli**

461 Original recordings consisted of a set of 474 monosyllabic French words, spoken to a metronome at  
462 a rate of 2-Hz by a male, native French speaker. This approach aligned perceptual centers (p-cen-  
463 ters)<sup>69</sup> of the words to the metronome beat and resulted in perceptually very rhythmic speech (see  
464 Zoefel et al<sup>70</sup> for a detailed description of stimuli and task). Stimuli were then time-compressed to 3-  
465 Hz using the pitch-synchronous overlap and add (PSOLA) algorithm implemented in the Praat soft-  
466 ware package, and the metronome beat was made inaudible to participants. Intelligibility of the  
467 speech recordings was degraded by applying 16-channel noise-vocoding<sup>71</sup>. 16-channel noise-vo-  
468 coded speech is not as easy to understand as clear speech, but is still clearly intelligible<sup>72</sup>. Individual,  
469 noise-vocoded words were then concatenated into a continuous sound stream of 5-min length (i.e.,

470 totaling 900 words). The order of words was randomized with a constraint such that every word from  
471 the stimulus set had occurred before it can be repeated. Across all blocks, 150 target words that  
472 deviated from the 3-Hz stimulus rate by 80-ms (50% presented early, 50% late) were embedded into  
473 the rhythmic speech stream (25 targets per block, 75 targets per eyes-open/eyes-closed condition).  
474 Participants were asked to indicate violations of the rhythm by pressing the space bar on a standard  
475 computer keyboard.

476 The experiment was carried out in a dimly-lit recording chamber, separated from the experimenter.  
477 Audio signals were generated in MATLAB 2019a and streamed to a Fireface UCX (RME Audio,  
478 Heimhausen, Germany) soundcard. The audio stream was presented to participants using a pneu-  
479 matic In-Ear headphone system (Etymotic Research ER-2, Etymotic Research Inc., USA). This sys-  
480 tem provides an additional layer of shielding from environmental noise. Experimental instructions  
481 were given via a computer screen in the experimental room controlled using Psychtoolbox 3 for  
482 MATLAB. During blocks that required participants to keep their eyes open, a white fixation cross was  
483 presented on a black background at the center of the screen. The fixation cross was also shown  
484 during eyes-closed conditions to keep environmental light conditions constant across blocks.

## 485 **EEG**

486 Electroencephalogram was recorded from 64 active electrodes according to the extended interna-  
487 tional 10-10 system using a BioSemi Active 2 amplifier (BioSemi, Amsterdam, Netherlands). EEG  
488 signals were recorded at a rate of 2048-Hz and digitally stored on a hard drive using ActiView v9.02  
489 Software (BioSemi, Amsterdam, Netherlands). Electrodes were mounted in an elastic cap and con-  
490 nected to participants' scalps via a conductive gel (Signa Gel, Parker Laboratories Inc., Fairfield, NJ,  
491 USA). Signal offsets of the system were kept below 50- $\mu$ V.

## 492 **EEG processing**

493 EEG analyses were performed in MATLAB 2019b using the fieldtrip toolbox<sup>73</sup>. Data was re-refer-  
494 enced to common average, resampled to 256-Hz and filtered between 1-Hz and 40-Hz using a two-  
495 pass, 4-th order, zero-phase Butterworth filter. An independent component analysis was performed  
496 to project out artifacts related to eye-blinks, movements, heart-beat or muscular activity.

497 Signals were then epoched into consecutive, overlapping segments centered around the p-center  
 498 (the part of the word that was centered on the metronome beat) of each word ( $\pm 1$ -sec). Each seg-  
 499 ment was 2-sec long and therefore comprised seven p-centers (**Fig. 1**). The use of segments allowed  
 500 us to extract time-resolved measures of  $\alpha$ -oscillations and neural entrainment.

501 A Fast-Fourier Transform (FFT, Hanning window, 2-sec zero padding) was applied on each of the  
 502 segments. The resulting complex Fourier coefficients were used to extract power in the  $\alpha$ -band (8-  
 503 12-Hz) as well as inter-trial coherence (ITC) at the stimulus rate (3-Hz). In line with previous work<sup>10,23</sup>,  
 504 we used ITC to quantify neural entrainment to speech, i.e. neural activity aligned to the 3-Hz rhythm.  
 505 ITC quantifies phase consistency across trials (here: segments). ITC was computed in sliding win-  
 506 dows comprising 15 segments (step size: 1 segment). Note that, due to the overlap between suc-  
 507 cessive segments, this window is 5 seconds long. We used the following equation to compute ITC  
 508 in each time window:

$$509 \quad ITC(f) = \left| \frac{1}{N} \sum_{n=1}^N e^{-i(\varphi(f,n))} \right|$$

510 where  $\varphi(f, n)$  is the phase in segment  $n$  at frequency  $f$ .  $N$  corresponds to the number of segments  
 511 in the window.  $f$  was therefore set to 3-Hz and  $N$  was set to 15. Within the same windows we aver-  
 512 aged power spectra across segments to ensure consistent temporal smoothing in both measures.  
 513 Power and ITC spectra were visually inspected to ensure good ratio between spectral peaks and the  
 514 “noise” at the surrounding frequencies as well as to ensure plausible topographies.

515 This approach yielded neural measures as a function of time: One  $\alpha$ -power, and one ITC value per  
 516 time window. We then used these time-resolved measures to extract their fluctuations over time. ITC  
 517 and  $\alpha$ -power time-series were first z-transformed to ensure comparable amplitudes. They were then  
 518 divided into 100-sec segments with 90% overlap. This resulted in a total of 60 segments across the  
 519 3 blocks per condition (eyes-open vs. eyes-closed). Finally, the segments were submitted to another  
 520 FFT (hanning window, 400-sec zero padding). Length of the segments and padding were chosen to  
 521 ensure sufficient spectral resolution below 0.2-Hz as well as a sufficient number of phase estimates  
 522 to quantify if there is systematic coupling between signals. Importantly, a 90% overlap results in an  
 523 effective step size of 10-sec in our case. Given our aim to analyze fluctuations at rates below 0.2-Hz

524 (i.e., slower than 5-sec), a 10-sec step size is sufficient to include 0.5 – 2 new cycles of such slow  
525 fluctuations. To rule out that these step and window size parameters affect our results we repeated  
526 the analysis using shorter segments (50-sec with 90% overlap, i.e., 5-sec time-steps). Overall, we  
527 obtained very similar results compared to the main analysis.

528 The obtained low-frequency spectra were corrected for arrhythmic (“1/f”) activity using the foof al-  
529 gorithm<sup>74</sup> as shipped with the fieldtrip toolbox. This step helped improve the identification of peaks  
530 in the spectrum and revealed prominent spectral peaks in the  $\alpha$ -power and ITC time-courses. On the  
531 group level, these peaks were close to 0.07-Hz for both  $\alpha$ -power and ITC (**Fig. 2a**). We next identified  
532 individual peak frequencies of  $\alpha$ -power and ITC fluctuations. To do so, we selected the peak fre-  
533 quency that was closest to 0.07-Hz rhythm for individual participants (in a range of 0.04-Hz to 0.1-  
534 Hz). In accordance with Lakatos et al 2016<sup>10</sup>, we then used the individual peak frequency of the  $\alpha$ -  
535 power envelope to extract the phase of  $\alpha$ -power and ITC fluctuations in each 100-sec segment, and  
536 computed their phase difference. Phase differences were subsequently averaged across segments,  
537 separately for each subject and condition. To rule out that coupling between  $\alpha$ -power and entrain-  
538 ment are driven by entrainment effects at harmonic frequencies in the  $\alpha$ -band (9-Hz & 12-Hz), we  
539 repeated the analysis for the coupling between fluctuations in 3-Hz ITC and ITC at 9-Hz and 12-Hz.  
540 The results of this analysis are presented in **Supplementary Fig. S3**.

541 To investigate how  $\alpha$ -power and ITC fluctuations relate to the detection of target stimuli, we filtered  
542 the corresponding envelopes around the individual  $\alpha$ -power envelope peak frequency ( $\pm 0.02$ -Hz),  
543 identified in the previous step, using a causal, 6-th order, one-pass Butterworth filter. The causal  
544 filter was chosen to avoid contamination of pre-stimulus activity with stimulus related changes in  
545 brain activity. We epoched the signals from -14-sec to +7-sec around target stimuli. Using a Hilbert  
546 transform, we then extracted instantaneous phase angles over time and averaged them across trials,  
547 separately for ITC and  $\alpha$ -power fluctuations around hits and misses, respectively. Subsequently, for  
548 both  $\alpha$ -power and ITC fluctuations, we computed the time-resolved phase difference between hits  
549 and misses in the interval before target onset (-14-sec to -2.5-sec). The interval ends 2.5-sec prior  
550 to the onset of target stimuli to avoid including target-evoked brain responses, which can smear into  
551 the interval due to the symmetric 5-sec window (described above) that was used to compute ITC

552 values and to smoothen  $\alpha$ -power trajectories. The analysis was restricted to channels from signifi-  
553 cant clusters revealed in previous analyses (**Fig. 2d,e; Supplementary Table 1**).

#### 554 **Source analysis**

555 We applied dynamic imaging of coherent sources (DICS) beamforming<sup>31</sup> at individual peak frequen-  
556 cies of the slow fluctuations in  $\alpha$ -power and ITC. Leadfields were constructed from the standard  
557 boundary element model of the fieldtrip toolbox, and standardized electrode locations were defined  
558 in MNI space. We projected the complex Fourier coefficients from each 100-sec segment onto a  
559 surface grid with 20484 source locations. From these complex coefficients, we obtained a neural  
560 activity index by dividing oscillatory power by an estimate of the noise bias. To quantify coupling  
561 between  $\alpha$ -power and ITC fluctuations for different combinations of brain regions, we computed the  
562 phase angle of these two neural measures for each segment, source location, and subject. We then  
563 applied a parcellation into 360 regions of interest (ROIs) according to the HCP-MMP1 atlas of the  
564 human connectome project<sup>32</sup>. To this end, we computed the average phase across all source loca-  
565 tions within an ROI. We then computed the average phase across the 60 segments for each ROI  
566 and subject, separately for  $\alpha$ -power and ITC fluctuations, and tested for consistent phase relations  
567 between the two (our measure of connectivity) across subjects, as detailed below. The parcellation  
568 of source-level data reduces the number of channel-channel comparisons necessary and provides  
569 meaningful anatomical labels, thereby improving interpretability and reducing computational de-  
570 mands. It also mitigates localization errors arising from the use of standard head models and elec-  
571 trode locations for all participants, as brain activity is integrated over larger areas of the brain.

#### 572 **Behavioral analysis**

573 Average reaction times, as well as the proportion of hits, misses and false alarms were computed  
574 for each condition (eyes-open vs. eyes-closed). A target word was considered a hit, if a button was  
575 pressed within 2-sec after stimulus onset, otherwise it was considered a miss. Button presses oc-  
576 ccurring outside these response intervals were considered false-alarms. Hit rates were computed by  
577 dividing the number of responses to targets by the number of targets (75 per condition), false alarm

578 rates were computed by dividing responses outside of response intervals by the number of standards  
579 (2475 per condition).

## 580 **Statistical analyses & Reproducibility**

581 Statistical analyses were performed in Matlab 2019b using the circular statistics toolbox<sup>75</sup> in combi-  
582 nation with functions in fieldtrip for massive-multivariate permutation statistics<sup>73,76</sup>. All statistical anal-  
583 ysis were conducted on n=23 participants.

584 To assess whether there is a significant coupling between  $\alpha$ -power and entrainment fluctuations (i.e.  
585 envelopes), we tested if their phase difference shows a systematic clustering across subjects (i.e.  
586 differs from a uniform distribution). To this end, we first computed the average phase difference  
587 between  $\alpha$ -power and ITC envelopes (separately for each channel and subject as detailed in section  
588 4.5.1) and subjected them to Rayleigh's test for uniformity of circular data. This test yields a z-statistic  
589 (one per channel) which is high if these phase differences are non-uniformly distributed across sub-  
590 jects. We next tested whether there is a cluster of channels with such a non-uniform distribution. We  
591 randomly shuffled  $\alpha$ -power and ITC segments within subjects 10,000 times, re-computed the aver-  
592 age phase difference between the two signals per-subject and the corresponding Rayleigh's statistic  
593 on the group level, yielding 10,000 z-statistics per channel. Finally, we compared actual data with  
594 shuffled ones to obtain group-level p-values for channel clusters, using Monte Carlo estimates<sup>76</sup>.

595 A similar statistical approach was used to test for significant coupling of  $\alpha$ -power and ITC fluctuations  
596 in the parcellated source-level data. In contrast to the sensor level analysis, the test was run for all  
597 possible combinations of ROIs. To keep the resulting network structures sparse, we employed a  
598 more conservative  $\alpha$ -level of 0.01 for this test.

599 A significantly non-uniform distribution of phase differences between  $\alpha$ -power and ITC envelopes  
600 indicates that the two are coupled but does not tell us anything about their phase relation. If this  
601 phase relation is close to 0, this would speak against  $\alpha$ -oscillations and entrainment reflecting op-  
602 posing processing modes. We therefore tested the phase relation between the two deviates from  
603 zero within an identified channel cluster, using the `circ_mtest` function of the circular statistics  
604 toolbox. The function tests if a given angle lies within a given confidence interval (e.g., 95% or 99%)  
605 of a phase distribution. To estimate a p-value, we performed the test against different significance



606 levels ( $\alpha < .05$  and  $\alpha < .01$ ) and report the lowest significant  $\alpha$ -level for each comparison (i.e.,  $p < .05$   
607 or  $p < .01$ ), along with the circular average of the underlying phase distribution and the 95% or 99%  
608 circular confidence intervals (CI). Although a non-zero phase relation between  $\alpha$ -oscillations and  
609 entrainment might already indicate different modes of processing, our hypothesis was more explicit  
610 in that it assumes an opposing (i.e. anti-phase) relation between the two. To evaluate this hypothesis,  
611 we also report if the CIs cover  $\pm\pi$ .

612 Comparisons of peak frequencies, hit and false alarm rates and reaction times were performed in  
613 Matlab 2019b using dependent-samples t-tests.

#### 614 **Data availability**

615 The underlying anonymized data is available in minimally processed form (down sampled, filtered,  
616 artifacts suppressed with ica) via the open science framework (<https://osf.io/64ycj/>). Due to the file  
617 size, the unprocessed raw data can be obtained upon reasonable request from the corresponding  
618 authors.

#### 619 **Code availability**

620 The MATLAB code used to process and analyze the data is available via the same open science  
621 framework repository (<https://osf.io/64ycj/>).

#### 622 **Acknowledgements**

623 This research was supported by a grant from the Agence Nationale de la Recherche (grant number  
624 ANR-21-CE37-0002) awarded to Benedikt Zoefel.

#### 625 **Author contributions**

626 **Florian H. Kasten:** Conceptualization, Methodology, Software, Data Collection, Formal Analysis,  
627 Investigation, Writing – Original Draft, Visualization, **Quentin Busson:** Data Collection, Software,  
628 Writing – Review & Editing, **Benedikt Zoefel:** Conceptualization, Writing – Review & Editing, Super-  
629 vision, Funding Acquisition

630 **Conflict of interest**

631 FHK, QB, and BZ declare no competing interests.

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- 839

840 **Tables**841 **Table 1**842 *Regions according to HCP-MMP1 atlas showing auditory entrainment or  $\alpha$ -power coupling.*

<b>Cortical structure</b>	<b>Measure</b>	<b>ROIs</b>	<b>Hemisphere</b>
Medial temporal	ITC	Hippocampus, Para-Hippocampal Area 3, Area TF, Para-Hippocampal Area 2	L
Lateral Temporal	ITC	Area TE1 Middle, Area TG dorsal	L
Inferior Frontal	ITC	Area 47l (47 lateral), Area anterior 47r,	L
Orbital and Polar Frontal	ITC	Area 13l, Area 47s, Area 47m	L
Posterior Opercular	ITC	Area OP4-PV	R
Early Auditory	ITC	Para-Belt Complex, Medial Belt Complex	R
Auditory Association	ITC	Area STSd posterior, Area STSv posterior, Auditory 4 Complex	R
Temporo-Parieto-Occipital Junction	ITC	Area Temporo-Parieto-Occipital Junction 1	R
Lateral Temporal	ITC	Area TE1 Middle	R
Posterior Cingulate	alpha	Retro-Splenial Complex, Pre-Cuneus Visual Area, Area dorsal 23 a+b, Area 31p ventral, Area 31pd, Area 31a	L
Paracentral Lobular & Mid Cingulate	alpha	Area 5L	L
Superior Parietal	alpha	Lateral Area 7A, Medial Area 7A	L
Ventral Stream Visual	alpha	Fusiform Face Complex, Ventro-Medial Visual Area 1, Ventral Visual Complex	L
Medial Temporal	alpha	Pre-Subiculum, Para-Hippocampal Area 1	L
Premotor	alpha	Premotor Eye Field, Area 55b, Rostral Area 6	R
Posterior Cingulate	alpha	Pre-Cuneus Visual Area, Area dorsal 23 a+b, Area 31a, Pro-Striate Area	R
Paracentral Lobular & Mid Cingulate	alpha	Area 5m, Area 5L	R
Dorsolateral Prefrontal	alpha	Area 8C	R
Inferior Frontal	alpha	Area 44, Area IFJa	R
Posterior Opercular	alpha	Area OP2-3-VS	R
Ventral Stream Visual	alpha	Ventro-Medial Visual Area 1	R

843 *Note.* Overview of cortical structures with ROIs that show auditory entrainment or  $\alpha$ -power fluctuations significantly coupled  
844 to other ROIs. Labels are according to the HCP-MMP1 atlas. *Measure* indicates if ROIs show ITC coupled to  $\alpha$ -power in  
845 other ROIs (*ITC*) or  $\alpha$ -power coupled to ITC in other ROIs (*alpha*). Hemisphere labels correspond to: L = left, R = right.

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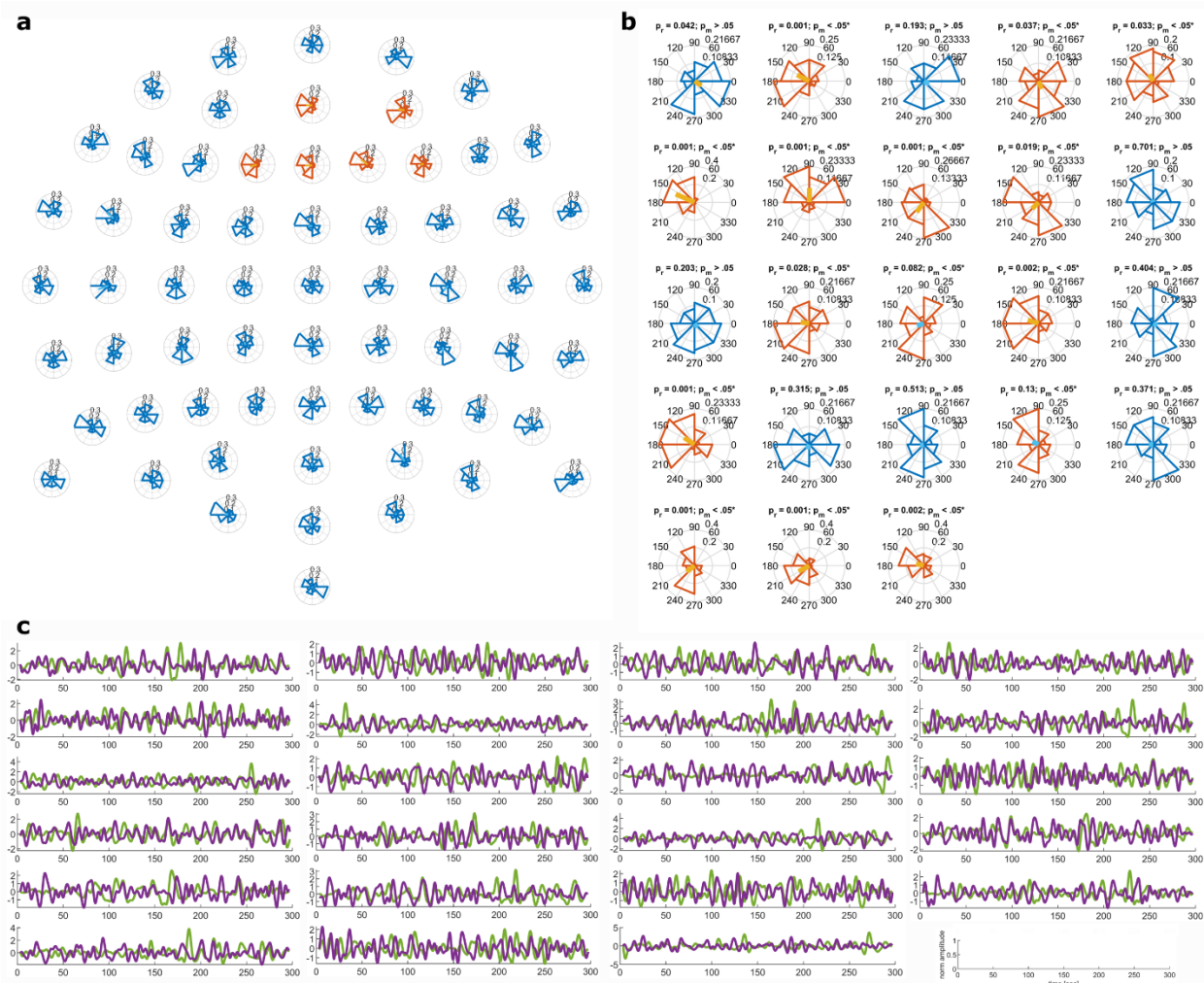
865 **Supplementary Information: Opposing neural processing modes**

866 **during auditory sustained attention alternate rhythmically**

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869 **1 Supplementary Figures**

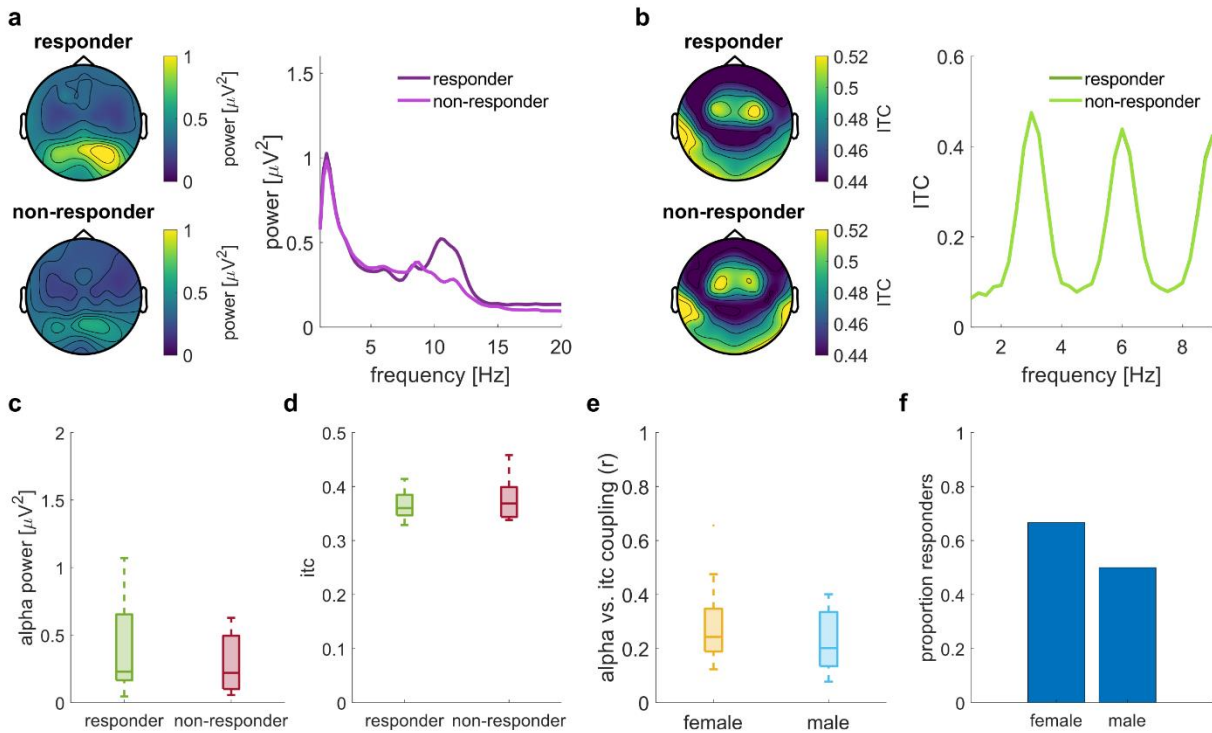


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871 **Supplementary Figure S6:  $\alpha$ -power and entrainment coupling for individual channels and participants.**  
 872 **(a + b)** Distributions of phase differences between  $\alpha$ -power and entrainment fluctuations. (a) shows these  
 873 distributions across participants but separately for each channel. Distributions in orange indicate channels  
 874 forming the significant cluster revealed by the permutation Rayleigh test (Fig. 2d in the main manuscript). Anti-  
 875 phase coupling appears to be consistent across channels within the cluster. (b) shows distributions for individ-  
 876 ual subjects, within the significant channel cluster. Above the individual panels are shown results from single-  
 877 subject Rayleigh's test ( $p_r$ ) for non-uniformity computed across 60 overlapping 100-sec segments, and from  
 878 test comparing the trial-averaged angle against 0 ( $p_m$ ). 14 out of 23 participants exhibit a significant coupling  
 879 between  $\alpha$ -power and entrainment fluctuations at an  $\alpha$ -level of 0.05. 15 out of 23 participants further exhibit an  
 880 average phase difference that is significantly different from 0. Phase distributions with significant coupling are  
 881 indicated by a yellow average phase vector. Distributions significantly differing from zero are shown in orange.  
 882 Importantly, there is a strong overlap between subjects showing significant coupling of the signals, and those  
 883 showing an average phase difference significantly different from zero. (c) Exemplary  $\alpha$ -power and entrainment  
 884 time-courses. Traces depict fluctuations of  $\alpha$ -power (green) and auditory entrainment (violet) over time for an  
 885 exemplary experimental block with eyes-open for each participant. For display purposes, the traces were fil-  
 886 tered between 0.03-Hz and 0.2-Hz. Axis labels are indicated in the lower right plot.

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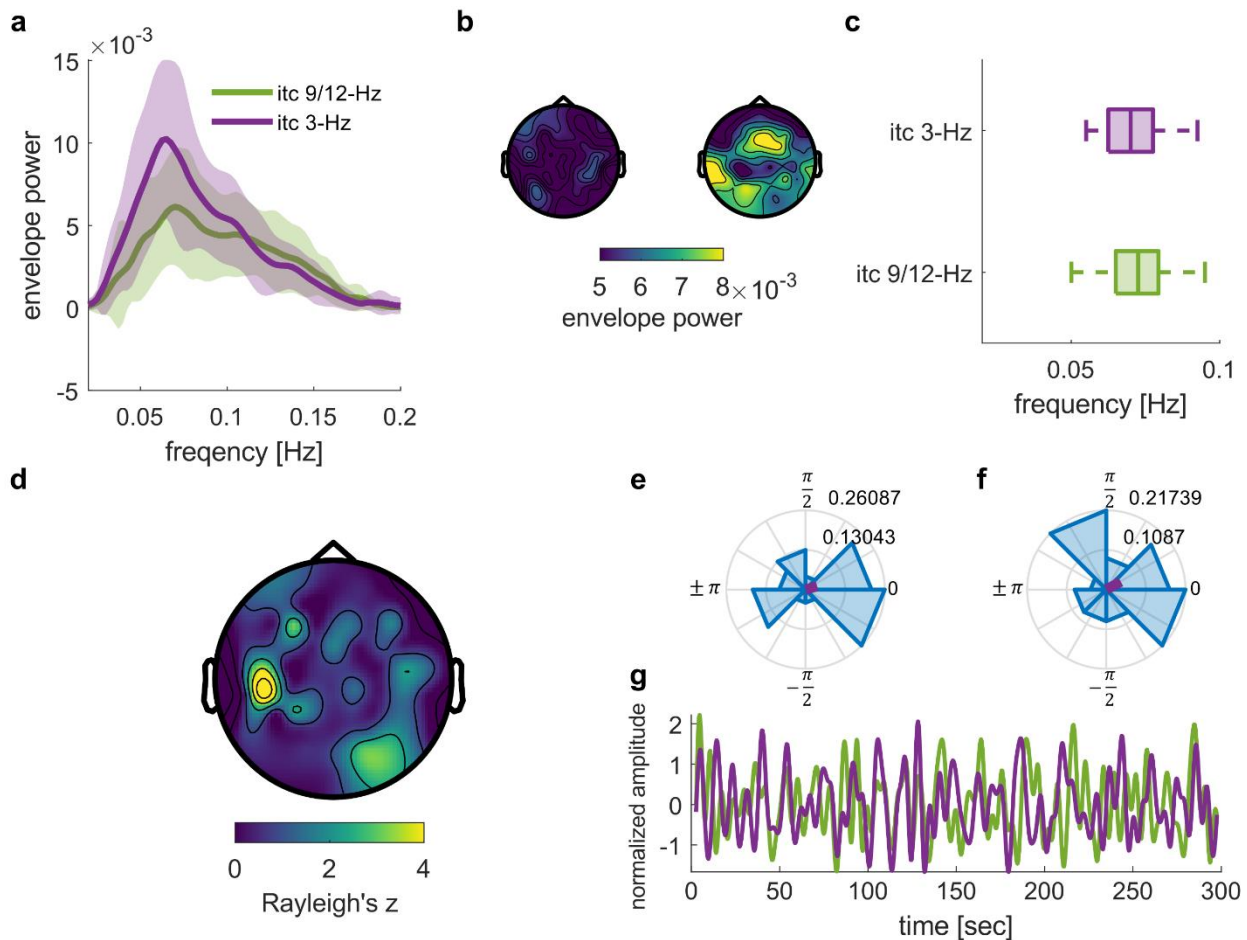


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890 **Supplementary Figure S7: Responder/Non-responder analysis (eyes-open condition).** (a) Topography  
 891 of average  $\alpha$ -power for responders (top left) and non-responders (bottom left). The power spectrum on the  
 892 right depicts the average power spectra of responders and non-responders within the cluster of electrodes  
 893 showing significant  $\alpha$ -power and ITC coupling (Fig. 2e in main manuscript). (b) Topography of 3-Hz ITC for  
 894 responders (top left) and non-responders (bottom left). The ITC spectrum on the right depicts the average ITC  
 895 across frequencies within the cluster of electrodes showing significant  $\alpha$ -power and ITC coupling (Fig. 2d in  
 896 the main manuscript). (c) Boxplots depict the distribution of  $\alpha$ -power within the cluster of electrodes showing  
 897 significant coupling to ITC for responders and non-responders. Panel (d) depicts the same distribution for ITC  
 898 values. (e) Distribution of  $\alpha$ -power and coupling (r, cf. Supplementary Fig. S1b), separately for male and female  
 899 participants. (f) Proportion of male and female participants showing significant  $\alpha$ -power and ITC coupling.

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902 **Supplementary Figure S8: Control analysis for coupling between 3-Hz entrainment and entrainment at**  
 903 **harmonic frequencies that lie in the  $\alpha$ -band (9-Hz and 12-Hz).** To rule out that the coupling between  $\alpha$ -  
 904 band power and 3-Hz entrainment is driven by entrainment effects at harmonic frequencies within the  $\alpha$ -band,  
 905 we repeated the analysis described in the main manuscript. However, instead of using  $\alpha$ -power fluctua-  
 906 tions, we tested whether 3-Hz ITC fluctuations are coupled with ITC fluctuations at harmonics of 3 Hz and that  
 907 lie in the  $\alpha$ -band (9-Hz and 12-Hz). **(a)** The resulting spectra show a substantially reduced rhythmic activity  
 908 compared to the fluctuations in  $\alpha$ -power (Fig. 2a). **(b)** Topography of fluctuations in 9-Hz and 12-Hz ITC (left)  
 909 as well as 3-Hz ITC (right, corresponding to Fig. 2b in main manuscript). **(c)** Distribution of peak frequencies  
 910 in the spectra of  $\alpha$ -power and ITC envelopes. **(d)** Permutation cluster analysis does not reveal any significant  
 911 coupling between 3-Hz and 9-Hz & 12-Hz ITC envelopes ( $p_{\text{cluster}} > .17$ ). **(e+f)** Distribution of phase differences  
 912 between 3-Hz and 9-Hz & 12-Hz ITC fluctuations, within the clusters that show significant coupling between  $\alpha$ -  
 913 power and 3-Hz ITC (Fig. 2d). We did not find evidence that these phases significantly differ from 0 (circular  
 914 one-sample test against angle of zero:  $p > .05$ ,  $M_{\text{angle}} = 0.28$  rad, and  $p > .05$ ,  $M_{\text{angle}} = 0.49$  rad). **(g)** exemplary  
 915 time-course of 3-Hz vs. 9-Hz + 12-Hz ITC fluctuations. Overall, these results do not support the idea that  
 916 harmonic entrainment in the  $\alpha$ -band gives rise to the coupling between  $\alpha$ -power fluctuations and auditory en-  
 917 trainment.

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926 **2 Supplementary Tables**

927 **Supplementary Table 1:** *Composition of clusters with significant entrainment vs. alpha power coupling in*  
 928 *permutation cluster analysis*

Cluster	Channels	p <sub>cluster</sub>
ROI1: entrainment vs. alpha per channel (Fig. 2d)	F1, AF4, AFz, Fz, F2, F4	.037
ROI 2: entrainment in ROI 1 vs. alpha per channel (Fig. 2e)	Fp1, AF3, F1, FC1, C3, CP3, P3, Pz, CPz, Fpz, Fp2, AF4, AFz, Fz, F2, F4, F6, FC6, FC2, FCz, Cz, P2, P4, PO4	.042

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930 **3 Supplementary Notes**931 **Supplementary Note 1**

932 In an exploratory follow-up analysis, we contrasted various oscillatory features in EEG data from  
 933 participants which exhibit coupling between  $\alpha$ -power and entrainment fluctuations (15 “responders”  
 934 in **Supplementary Fig. S1b**) with features from those who did not (8 “non-responders” in Supple-  
 935 mentary Fig. S1b). Responders exhibited numerically higher power in the  $\alpha$ -band (Supplementary  
 936 Fig. S2a,c) despite near-identical ITC (**Supplementary Fig. S2b,d**). However, when we compared  
 937  $\alpha$ -power within the significant cluster that showed coupling to ITC (cf. Fig. 2e), this difference did not  
 938 reach significance (responder vs non-responder  $\alpha$ -power:  $t_{21} = 0.75$ ,  $p = .46$ ; ITC:  $t_{21} = -0.74$ ,  $p =$   
 939  $0.47$ ; independent samples t-test). There was no reliable difference in  $\alpha$ -power and ITC coupling  
 940 between male and female participants ( $t_{21} = 0.95$ ,  $p = .35$ , independent samples t-test; Supplemen-  
 941 tary Fig. S2e,f)

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