

1 **Title Page**

2 **Title**

3 The impact of eye closure on anticipatory alpha activity in a tactile discrimination task

4 **Abbreviated title**

5 Effect of eye closure on anticipatory alpha

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18 **Conflict of interest statement**

19 The authors declare that the research was conducted in the absence of any commercial or financial

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21

## 22 Abstract

23 One of the very first observations made regarding alpha oscillations (8–14 Hz), is that they increase  
24 in power over posterior areas when awake participants close their eyes. Recent work, especially in  
25 the context of (spatial) attention, suggests that alpha activity reflects a mechanism of functional  
26 inhibition. However, it remains unclear how eye closure impacts anticipatory alpha modulation  
27 observed in attention paradigms, and how this affects subsequent behavioral performance. Here,  
28 we recorded magnetoencephalography (MEG) in 33 human participants performing a tactile  
29 discrimination task with their eyes open vs. closed. We replicated the hallmarks of previous  
30 somatosensory spatial attention studies: alpha lateralization across the somatosensory cortices as  
31 well as alpha increase over posterior regions. Furthermore, we found that eye closure leads to (i)  
32 reduced task performance, (ii) widespread increase in alpha power, and (iii) reduced anticipatory  
33 visual alpha modulation (iv) with no effect on somatosensory alpha lateralization. Regardless of  
34 whether participants had their eyes open or closed, increased posterior alpha power and  
35 somatosensory alpha lateralization improved their performance. Thus, we provide evidence that  
36 eye closure does not alter the impact of anticipatory alpha modulations on behavioral  
37 performance. We propose there is an optimal posterior alpha level for somatosensory task  
38 performance, which can be achieved through a combination of eye closure and top-down  
39 anticipatory attention.

40

## 41 Significance Statement

42 Alpha oscillations are dominant when awake participants have their eyes closed. Furthermore,  
43 alpha is known to modulate with anticipatory attention, and has been ascribed a role of active  
44 functional inhibition. Surprisingly, the link between anticipatory alpha and eye closure remains  
45 unclear. Here we collected MEG data while human participants performed a tactile discrimination  
46 task either with their eyes open or closed. Eye closure led to a widespread increase in alpha power,  
47 and affected anticipatory visual alpha modulation but not somatosensory alpha lateralization.  
48 Importantly, eye closure did not affect the correlation between alpha and task performance. Our  
49 findings provide novel insights into how eye closure impacts anticipatory alpha modulation, and  
50 how optimal alpha levels for task performance can be achieved differently.

51

## 52 Introduction

53 Since the discovery of the cortical alpha rhythm by Hans Berger (1929) almost a century ago, it has  
54 been known that a general increase of posterior alpha power occurs when awake participants close  
55 their eyes (Adrian & Matthews, 1934). While traditionally the alpha rhythm was associated with a  
56 state of cortical idling (Pfurtscheller et al., 1996), more recent work suggests that alpha activity  
57 reflects a mechanism of functional inhibition (Foxe & Snyder, 2011; Haegens et al., 2011; Jensen &  
58 Mazaheri, 2010; Klimesch et al., 2007). In support of such an inhibitory mechanism, visual spatial  
59 attention is known to modulate alpha activity in a lateralized fashion: alpha decreases contralateral  
60 to the attended location (Sauseng et al., 2005) and increases contralateral to the ignored location,  
61 presumably to suppress distracting input (Kelly et al., 2009; Worden et al., 2000). This lateralized  
62 alpha activity correlates with visual detection performance (Händel et al., 2011; Thut et al., 2006).  
63 Similar patterns have been observed for the auditory (Banerjee et al., 2011; Frey et al., 2014; Straub  
64 et al., 2014; Wöstmann et al., 2016) and somatosensory domains (Anderson & Ding, 2011; Haegens  
65 et al., 2011, 2012; Jones et al., 2010).

66 Importantly, in our previous tactile spatial attention work, we found that somatosensory alpha  
67 lateralization was accompanied by an anticipatory increase of posterior alpha power, which  
68 positively correlated with tactile discrimination performance. We interpreted this posterior alpha  
69 increase to reflect a general inhibition of visual processing to improve tactile performance (Haegens  
70 et al., 2010, 2012). An obvious follow-up question is whether a similar posterior alpha increase, and  
71 accompanying tactile performance improvement, could be achieved by closing the eyes. Or, in  
72 other words, does the anticipatory task-related posterior alpha modulation stem from the same  
73 underlying sources as eye-closure related alpha modulation? Another question is how eye-closure

74 induced alpha increase relates to alpha lateralization patterns observed in the context of spatial  
75 attention.

76 Anecdotally, eye closure enhances the concentration on other sensory modalities by suppressing  
77 processing of visual input (Glenberg et al., 1998). Eye closure has been shown to boost stimulus  
78 responses in somatosensory areas (Brodoehl, Klingner, Stieglitz, et al., 2015; Götz et al., 2017), with  
79 mixed findings regarding impact on behavioral performance. To date, the relationship between  
80 eye-closure effects and anticipatory alpha modulation has only been investigated in the context of  
81 auditory attention: Wöstmann et al. (2020) showed that eye closure increases the general power of  
82 alpha oscillations, as well as the modulation of alpha during an auditory attentional task; however,  
83 this had no impact on behavioral performance.

84 Here, we asked whether and how eye-closure induced alpha modulations interact with anticipatory  
85 alpha modulations and associated behavioral performance effects. We recorded MEG while  
86 participants performed an adapted version of the tactile discrimination task from Haegens et al.  
87 (2011), during eyes-open and eyes-closed conditions. First, we asked whether the often-reported  
88 eye-closure related power increase extends beyond posterior alpha. Next, we compared the  
89 previously reported anticipatory alpha modulations—i.e., somatosensory alpha lateralization and  
90 visual alpha increase (Haegens et al., 2012, 2012)—between eye conditions and asked how they  
91 interact with the eye-closure related power increase. Finally, we asked whether the relationship  
92 between these alpha modulations and task performance differs across eye conditions; specifically,  
93 whether visual alpha increase (which we previously interpreted as inhibition of visual processing) is  
94 behaviorally relevant in the absence of visual input.

95

## 96 **Materials and Methods**

### 97 **Participants**

98 Participants were 34 healthy adults (Age:  $M = 25$ ,  $SD = 3.86$ , range = 20–33 years; 18 female; 30  
99 right handed, 2 left handed, 2 ambidextrous) without neurological or psychiatric disorders, who  
100 reported normal hearing and normal or corrected-to-normal vision. The study was approved by the  
101 local ethics committee (CMO 2014/288 “Imaging Human Cognition”) and in accordance with the  
102 Declaration of Helsinki. Participants gave written informed consent and were remunerated for their  
103 participation. One participant was excluded from analysis due to poor data quality.

### 104 **Experimental design**

105 Participants performed a tactile discrimination task (Figure 1; task adapted from Haegens et al.,  
106 2011) while their brain activity was recorded using MEG. Participants received an electrical stimulus  
107 (pulse train of a low or high frequency) to either the right or left thumb. Participants were  
108 instructed to determine as fast and accurately as possible whether the perceived stimulus was of  
109 low or high frequency, responding via button press with their right index finger (left button press  
110 indicated the low frequency; right button press indicated the high frequency). Prior to the stimulus  
111 presentation, an auditory cue (verbal “right” or “left”) directed participants’ attention to either  
112 their right or left hand. Spatial cues were always valid. Each trial started with a pre-cue interval of  
113 1.2 s followed by the auditory cue (0.2 s), a jittered 1–1.8 s pre-stimulus interval, the tactile  
114 stimulus (0.24-s pulse train), a response window of maximum 1.5 s, and finally auditory feedback  
115 indicating whether the answer was correct or incorrect.

116 Participants performed this task under two conditions: an eyes-open (EO) and an eyes-closed  
117 condition (EC). Conditions were presented in a counter-balanced block-design of four blocks per

118 condition with 76 trials each, resulting in a total of 304 trials per condition. During the EO condition,  
119 participants were instructed to fixate on a fixation cross in the middle of the screen. For the EC  
120 condition, participants kept their eyes closed for the duration of the block. After each block,  
121 participants were presented with a short questionnaire to rate their sleepiness level (very sleepy,  
122 sleepy, awake, very awake). Prior to the experiment, participants performed four training blocks  
123 (two per condition, 12 trials per block), during which they were familiarized with the task.

## 124 **Stimulus presentation**

125 We used the same setup as in Haegens et al. (2011): Electrical stimuli were delivered with two  
126 constant-current high-voltage stimulators (Digitimer Ltd, Model DS7A) to the right and left thumb.  
127 The intensity ( $M_{\text{right}} = 6.4$  mA, range = 3.9–9.5 mA;  $M_{\text{left}} = 5.5$  mA, range = 3.2–9.9 mA) of the 0.2-ms  
128 electric pulses was set to 150% of the participant's sensory threshold level. This level was  
129 established during a practice session before the recordings, for each thumb independently. Low  
130 (either 25 or 33.3 Hz) and high frequencies (41.7, 50, or 66.7 Hz) were determined for each  
131 participant individually to ensure successful execution of the task, above chance level but below  
132 ceiling performance. Auditory cues and feedback (0.2-s length each) were computer-generated and  
133 presented binaurally through air-conducting tubes.

## 134 **Data acquisition**

135 Whole-head MEG data were acquired at a sampling frequency of 1200 Hz with a 275-channel MEG  
136 system with axial gradiometers (CTF MEG Systems, VSM MedTech Ltd.) in a magnetically shielded  
137 room. Six permanently faulty channels were disabled during the recordings, leaving 269 recorded  
138 MEG channels. Three fiducial coils were placed at the participant's nasion and both ear canals, to  
139 provide online monitoring of participant's head position (Stolk et al., 2013) and offline anatomical  
140 landmarks for co-registration. Eye position was recorded using an eye tracker (EyeLink, SR Research

141 Ltd.). Upon completion of the MEG session, participant's head shape and the location of the three  
142 fiducial coils were digitized using a Polhemus 3D tracking device (Polhemus, Colchester, Vermont,  
143 United States). Anatomical T1-weighted MRIs were obtained during a separate session. To improve  
144 co-registration of the MRIs and MEG data, earplugs with a drop of Vitamin E were placed at  
145 participant's ear canals during MRI acquisition. These anatomical scans were used for source  
146 reconstruction of the MEG signal.

### 147 **Pre-processing**

148 MEG data were preprocessed offline and analyzed using the FieldTrip toolbox (Oostenveld et al.,  
149 2011) and custom-built MATLAB scripts. The MEG signal was epoched based on the onset of the  
150 somatosensory stimulus ( $t = -4$  to  $3$  s). The data were downsampled to a sampling frequency of 300  
151 Hz, after applying a notch filter to remove line noise and harmonics (50, 100, and 150 Hz). Bad  
152 channels and trials were rejected via visual inspection before independent component analysis  
153 (Jung et al., 2001) was applied. Subsequently, components representing eye-related and heart-  
154 related artefacts were projected out of the data (on average, eight components were removed per  
155 participant). Finally, for the resulting data, outlier trials of extreme variance were removed. This  
156 resulted in an average of 537 ( $\pm 7$  SEM) trials and 268 channels per participant for the reported  
157 analyses.

### 158 **Spectral analysis**

159 First, we calculated the planar representation of the MEG field distribution from the single-trial  
160 data using the nearest-neighbor method. This transformation makes interpretation of the sensor-  
161 level data easier as the signal amplitude is typically maximal above a source. Next, we computed  
162 spectral representations for two 1-s time windows: the pre-stimulus window and the pre-cue  
163 window, aligned to stimulus and cue onset, respectively. Each window was multiplied with a



164 Hanning taper, and power spectra (1–30 Hz; 1-Hz resolution) were computed using a fast Fourier  
165 transform (FFT) approach. Additionally, for a time-resolved-representation of the spectral power  
166 distribution, we computed time-frequency representations (TFRs) of the power spectra for the full  
167 trials per experimental condition. To this end we used an adaptive sliding time window of five  
168 cycles length per frequency ( $\Delta t = 5/f$ ; 20-ms step size).

### 169 **Alpha peak frequency**

170 In order to investigate how eye closure impacts alpha activity we computed the individual alpha  
171 peak frequencies for each participant, separately for occipital and centroparietal sensor-level  
172 regions of interest (ROIs), and separately for the EO and EC conditions. We determined participants'  
173 peak frequencies within a broad alpha range (7–14 Hz) during the pre-stimulus interval (-1 to 0 s).  
174 As intra-individual alpha peaks did not significantly vary with condition ( $F(1, 32) = 0.46$ ,  $p = 0.5$ ,  
175 ANOVA) or ROI ( $F(1, 32) = 1.04$ ,  $p = 0.31$ ), nor their interaction ( $F(1, 32) = 0.17$ ,  $p = 0.67$ ), we  
176 computed one average peak for each participant ( $M = 10$  Hz, range = 7–13 Hz). Using individual  
177 alpha peak frequency allows taking into account inter-individual variability, and provides a more  
178 accurate estimation of alpha activity than when using a fixed frequency band (Haegens et al., 2014).  
179 All further analysis was computed using these individual alpha peaks, with spectral bandwidth of  $\pm 1$   
180 Hz, unless indicated otherwise.

### 181 **Statistical analysis**

182 In order to investigate whether power differences between the EO and the EC conditions were  
183 significant, we used nonparametric cluster-based permutation tests (Maris & Oostenveld, 2007). In  
184 brief, this test first calculates paired t-tests for each sensor at each time and/or frequency point,  
185 which are then thresholded at  $p < 0.05$  and clustered on the basis of spatial, temporal, and/or  
186 spectral adjacency. The sum of t-values within each cluster is retained, and the procedure is

187 repeated 1000 times on permuted data in which the condition assignment within each individual is  
188 randomized. On each permutation, the maximum sum is retained. Across all permutations, this  
189 yields a distribution of 1000 maximum cluster values. From this distribution, the probability of each  
190 empirically observed cluster statistic can be derived (evaluated at  $\alpha = 0.05$ ).

191 We used this permutation test to investigate the impact of eye closure on (i) global oscillatory  
192 power, by contrasting power in the pre-stimulus interval between eye conditions, (ii) anticipatory  
193 visual alpha activity, by contrasting pre-stimulus baseline-normalized power between eye  
194 conditions, for each cue separately, and (iii) somatosensory alpha activity, by contrasting the pre-  
195 stimulus attention modulation index, calculated as  $(\text{attention-left} - \text{attention-right}) / (\text{attention-left}$   
196  $+ \text{attention-right})$  between eye conditions.

197 In order to investigate the impact of pre-stimulus alpha activity on behavioral performance, we  
198 focused our analysis on visual and somatosensory ROIs that were defined in sensor space. For the  
199 somatosensory ROIs, our selection was data-based, i.e., per hemisphere we selected 10 sensors  
200 with the maximum evoked response to contralateral tactile stimulation. For the visual ROIs, as our  
201 design lacked visual stimuli, our selection included 10 left and 10 right occipital sensors. One  
202 participant was excluded from analysis due to poor data quality. Note that for alpha power in the  
203 visual ROIs, we use the term “absolute” modulation to denote overall non-baseline-normalized  
204 power in the pre-stimulus window, while the term “anticipatory” denotes the baseline-normalized  
205 power in the same pre-stimulus window.

## 206 **Alpha lateralization index**

207 To capture the relative pre-stimulus somatosensory alpha distribution over both hemispheres in  
208 one measure, we computed a lateralization index of alpha power (Haegens et al., 2011; Thut et al.,  
209 2006) for each participant, using individual somatosensory ROIs: alpha lateralization index = (alpha-

210 ipsilateral - alpha-contralateral) / (alpha-ipsilateral + alpha-contralateral). This index gives positive  
211 values if alpha power is higher over the ipsilateral hemisphere and/or lower over the contralateral  
212 hemisphere (with contra- and ipsilateral sides defined with respect to the spatial cue). Negative  
213 values arise if alpha power activity is lower over the ipsilateral hemisphere and/or higher over the  
214 contralateral hemisphere.

## 215 **Source reconstruction**

216 In order to localize the generators of the sensor-level spectrotemporal effects, we applied the  
217 frequency-domain adaptive spatial filtering technique of dynamical imaging of coherent sources  
218 (Gross et al., 2001). For each participant, an anatomically realistic single-shell headmodel based on  
219 individual T-1 weighted anatomical images was generated (Nolte, 2003). The brain volume of each  
220 individual subject was divided into a grid with a 0.5-cm resolution and normalized toward a  
221 template MNI brain using non-linear transformation. For each grid point, leadfields were computed  
222 with a reduced rank, which removes the sensitivity to the direction perpendicular to the surface of  
223 the volume conduction model. This procedure ensures that each grid-point represents the same  
224 anatomical location across all participants by taking into account the between-subject difference in  
225 brain anatomy and head shape.

226 Data from all conditions of interest were concatenated in order to compute the cross-spectral  
227 density (CSD) matrices (multitaper method (Mitra & Pesaran, 1999)). Leadfields for all grid points  
228 along with the CSD matrices were used to compute a common spatial filter (i.e., common for all  
229 trials and conditions) that was used to estimate the spatial distribution of power for time-frequency  
230 windows of interest highlighted in the previous analysis. The source orientation was fixed to the  
231 dipole direction with the highest strength.

232

## 233 Results

### 234 Eye closure impairs performance

235 Performance over all 33 participants for both eye conditions combined was an average accuracy of  
236 74.4% ( $SD = 9.96\%$ ) and an average reaction time (correct trials only) of 0.64 s ( $SD = 0.1$  s).  
237 Participants were more accurate ( $t(32) = 2.32$ ,  $p = 0.023$ , paired-test, mean EO = 75.7% + 9.9 SD,  
238 mean EC = 73.7% ± 9.9 SD) and faster ( $t(32) = -6.8$ ,  $p < 0.001$ , mean EO = 0.62 s ± 0.1 SD, mean EC =  
239 0.65 s ± 0.1 SD) at discriminating the frequency of the tactile stimuli in the EO condition in  
240 comparison to the EC condition (Figure 1B).

241 Further, we investigated the impact of eye closure (two levels: EC and EO) and block order (four  
242 levels: first, second, third and fourth) on the sleepiness score reported at the end of each block. We  
243 found a main effect of eye condition ( $F(1,26) = 9.7$ ,  $p = 0.004$ , ANOVA), with participants reporting  
244 being more awake when they had their eyes open. In addition, we found a main effect of block  
245 order ( $F(3,78) = 5.32$ ,  $p = 0.009$ ), with participants reporting being more awake in the first block in  
246 comparison to the second ( $t(26) = -3.15$ ,  $p = 0.014$ , posthoc paired t-test), third ( $t(26) = -3.45$   $p =$   
247 0.005) and fourth ( $t(26) = -3.15$ ,  $p = 0.014$ ), with no significant interaction ( $F(3,78) = 1.11$ ,  $p = 0.35$ ).  
248 Note that differences in sleepiness scores did not correlate with differences in behavioral  
249 performance between eye conditions (RT:  $r(26) = -0.19$ ,  $p = 0.32$ ; accuracy:  $r(26) = 0.22$ ,  $p = 0.25$ ).

### 250 Eye closure boosts global oscillatory activity

251 In order to investigate the impact of eye closure on overall oscillatory power, we contrasted power  
252 spectra (1–30 Hz) during the pre-stimulus window between the EO and the EC conditions (Figure 2).  
253 We found that power was higher for EC than EO (cluster-corrected  $p < 0.001$ ), both in the alpha (6–  
254 12 Hz) and in the beta range (17–30 Hz). The alpha cluster was widespread with a spectral peak at  
255 10 Hz, while the beta cluster was concentrated towards posterior sensors, showing the highest

256 difference between conditions around 20 Hz. While in this study we focused on alpha activity, as a  
257 control we compared event-related fields (ERFs) between eye conditions and found no differences  
258 (cluster-corrected  $p > 0.5$ ).

### 259 **Eye closure impacts anticipatory visual alpha modulation**

260 In order to investigate the impact of eye closure on anticipatory alpha modulation, we first  
261 contrasted alpha power between the pre-stimulus and the baseline windows. We found a pre-  
262 stimulus decrease of alpha power over left central sensors vs. baseline, for both EO and EC  
263 conditions (Figure 3AB; cluster-corrected  $p = 0.005$ ). Furthermore, we observed a pre-stimulus  
264 increase of posterior alpha power ( $p = 0.001$ ), which was exclusive to the EO condition. Next, we  
265 directly contrasted the baseline-normalized pre-stimulus alpha between EO and EC conditions,  
266 separately for each attention condition (i.e., attend left and right). For both attention conditions,  
267 we found higher posterior alpha power in the EO condition compared to the EC condition (cluster-  
268 corrected  $p < 0.001$ ; Figure 3CD). This result reflects an increase of visual alpha power during the  
269 pre-stimulus interval vs. baseline in the EO condition, an effect that was absent in the EC condition.  
270 Hence, despite an overall increase of alpha power with eye closure, the anticipatory posterior alpha  
271 modulation during the pre-stimulus interval was higher for open eyes.

### 272 **Eye-closure related and anticipatory alpha modulations are spatially distinct**

273 To address the question of whether eye-closure induced modulations and anticipatory alpha  
274 modulations share the same underlying cortical generators (i.e., localize to the same cortical  
275 regions), we compared the maxima of these effects in source space. For each participant, we  
276 identified the voxel displaying the maximal difference in absolute alpha power in the EO and the EC  
277 conditions, and the voxel displaying the maximal anticipatory pre-stimulus alpha power  
278 modulation. We then contrasted the x- y- and z- coordinates of these maxima using paired t-tests.

279 We found that maxima differed in their distribution along the y-axis ( $t(32) = -2.83$ ,  $p = 0.007$  paired  
280 t-test) and the z-axis ( $t(32) = -3.7$ ,  $p < 0.001$ ). In other words, maxima of the anticipatory alpha  
281 modulations were located more anterior and superior in comparison to the eye-closure induced  
282 modulations (Figure 4), with no differences in the distribution along the x-axis (i.e., left vs. right;  
283  $t(32) = 0.36$ ,  $p = 0.71$ ).

### 284 **Eye closure does not impact somatosensory alpha modulation**

285 In order to investigate how eye closure impacts anticipatory somatosensory alpha modulation, we  
286 contrasted the pre-stimulus attention modulation index (i.e., attention left vs. right) between EO  
287 and EC conditions. While there was a significant attention modulation—i.e., a pattern of lateralized  
288 sensorimotor alpha power (left increase  $p = 0.007$ ; right decrease  $p < 0.001$ ) when contrasting left  
289 vs. right attention conditions—no significant differences were found between eye conditions ( $p =$   
290  $0.34$ ; Figure 5). Thus, while both overall and anticipatory visual alpha activity differed between eye  
291 conditions, anticipatory somatosensory alpha modulation was not affected by eye closure.

### 292 **Eye closure does not impact the link between anticipatory alpha and** 293 **behavioral performance**

294 Finally, we investigated the impact of eye closure on the link between pre-stimulus alpha  
295 modulation and behavioral performance. First, we analyzed the relationship between pre-stimulus  
296 visual alpha power, both absolute (non-baseline normalized) and anticipatory (baseline-normalized)  
297 modulations, and performance, by binning the data based on correct vs. incorrect responses, and  
298 fast vs. slow RTs (divided by a median split).

299 For absolute visual alpha power and accuracy (Figure 6A), we found a significant main effect of  
300 accuracy ( $F(1, 31) = 15.2$ ,  $p < 0.001$ , ANOVA) with absolute visual alpha power being higher in  
301 correct trials in comparison to incorrect trials. In addition, we found a significant main effect of eye

302 condition ( $F(1, 31) = 26.92, p < 0.001$ ) and no significant interaction between eye condition and  
303 accuracy ( $F(1, 31) = 1.15, p = 0.29$ ). For absolute visual alpha power and RT (Figure 6B), we found a  
304 significant main effect of RT ( $F(1, 31) = 6.11, p = 0.02$ , ANOVA) with absolute visual alpha power  
305 being higher in fast trials in comparison to slow trials. In addition, we found a significant main effect  
306 of eye condition ( $F(1, 31) = 31.53, p < 0.001$ ) and no significant interaction between eye condition  
307 and RT ( $F(1, 31) = 0.65, p = 0.42$ ). In sum, absolute visual alpha power predicted more accurate and  
308 faster responses, regardless of eye condition.

309 For anticipatory visual alpha power and accuracy (Figure 6C), we found a significant main effect of  
310 accuracy ( $F(1, 31) = 4.84, p = 0.035$ , ANOVA) with anticipatory visual alpha power being higher in  
311 correct trials in comparison to incorrect trials. In addition, we found a significant main effect of eye  
312 condition ( $F(1, 31) = 69.88, p < 0.001$ ) and no significant interaction between eye condition and  
313 accuracy ( $F(1, 31) = 1.77, p = 0.19$ ). For anticipatory visual alpha power and RT (Figure 6D), we  
314 found a significant main effect of RT ( $F(1, 31) = 7.39, p = 0.01$ , ANOVA) with anticipatory visual  
315 alpha power being higher in fast trials in comparison to slow trials. In addition, we found a  
316 significant main effect of eye condition ( $F(1, 31) = 41.21, p < 0.001$ ) and no significant interaction  
317 between eye condition and RT ( $F(1, 31) = 1.04, p = 0.31$ ). In sum, anticipatory visual alpha  
318 modulation predicted more accurate and faster responses, regardless of eye condition.

319 For somatosensory alpha lateralization and accuracy (Figure 6E), we did not find a significant main  
320 effect of accuracy ( $F(1, 31) = 0.39, p = 0.53$ , ANOVA) nor a significant main effect of eye condition  
321 ( $F(1, 31) = 0.001, p = 0.98$ ), nor a significant interaction between eye condition and accuracy ( $F(1,$   
322  $31) = 1.19, p = 0.28$ ). For somatosensory alpha lateralization and RT (Figure 6F), we found a  
323 significant main effect of RT ( $F(1, 31) = 5.31, p = 0.027$ , ANOVA) with somatosensory alpha  
324 lateralization being higher for faster trials. We found neither a significant main effect of eye

325 condition ( $F(1, 31) = 2.47, p = 0.12$ ) nor a significant interaction between eye condition and RT ( $F$   
326  $(1, 31) = 0.001, p = 0.98$ ). In sum, somatosensory alpha lateralization predicted faster responses,  
327 regardless of eye condition.

328



## 329 Discussion

330 In a follow-up on our previous work (Haegens et al., 2010, 2011, 2012), we investigated how eye-  
331 closure related alpha modulations interact with anticipatory alpha dynamics and subsequent  
332 behavioral performance during a tactile spatial attention task. We found that task performance was  
333 reduced with eye closure. While eye closure led to a widespread increase in alpha power, this only  
334 affected anticipatory visual alpha modulation, with somatosensory alpha lateralization being the  
335 same across eyes-open and -closed conditions. Regardless of whether participants had their eyes  
336 open or closed, increases in posterior alpha power and somatosensory alpha lateralization  
337 improved their performance.

### 338 **Eye closure impacts global state**

339 Participants were less accurate and slower to discriminate tactile stimuli when their eyes were  
340 closed. While there have been several reports of a positive impact of eye closure on performance  
341 (e.g., perceptual sensitivity: Brodoehl, Klingner, Stieglitz, et al., 2015; memory retrieval: Parker &  
342 Dagnall, 2020; Vredeveltdt et al., 2011), other studies have reported no effects (e.g., memory  
343 retrieval: Bastarrika-Iriarte & Caballero-Gaudes, 2019; selective attention: Wöstmann et al., 2020)  
344 or negative impact (somatosensory discrimination Götz et al., 2017). Differences in paradigms  
345 (attention versus memory) and sensory modalities (auditory versus somatosensory) between these  
346 various reports renders it difficult to define common factors that govern the interaction between  
347 eye closure and behavioral performance. Nevertheless, Götz et al. (2017) argue that for tactile  
348 perception, eye closure might boost sensitivity but hinder discriminability, possibly due to the  
349 dependence of tactile discriminability upon extrastriate visual processing (Sathian & Zangaladze,  
350 2002). Following this logic, in our tactile discrimination task eye closure diminishes extrastriate  
351 visual processing, leading to worse behavioral performance.

352 Simultaneous with this behavioral deterioration, and as has been long known (e.g., Adrian &  
353 Matthews, 1934; Geller et al., 2014; Wöstmann et al., 2020), alpha power increased with eye  
354 closure. This increase was widespread, extending beyond occipital regions, and additionally  
355 included frequency ranges neighboring the alpha band (i.e., theta and beta). This observation  
356 supports the idea that eye closure does not only reflect a disengagement of visual areas, but rather  
357 a cortical state transition (Barry et al., 2007; Harris & Thiele, 2011; Marx et al., 2004). One  
358 interesting question is whether the observed oscillatory shifts are dependent on (lack of) light input  
359 or eye closure per se. Findings from resting state studies have been contradictory, with reports that  
360 alpha power is modulated by light input but not eye closure itself, and vice versa (Ben-Simon et al.,  
361 2013; Jao et al., 2013). Future research should investigate how light input impacts the interaction  
362 between eye closure and oscillatory dynamics during active tasks.

### 363 **Eye closure versus anticipatory attention**

364 Although eye closure led to a general increase of alpha power, we found a significant reduction of  
365 *anticipatory* visual alpha modulation in comparison to the eyes-open condition, with the maxima of  
366 this latter phenomenon extending more anterior than the global alpha increase. Somatosensory  
367 alpha lateralization was not affected by eye closure. These observed alpha modulations are in line  
368 with the proposal that alpha power reflects a functional mechanism of inhibition (Foxe & Snyder,  
369 2011; Haegens et al., 2011; Jensen & Mazaheri, 2010; Klimesch et al., 2007) that regulates cortical  
370 excitability to gate information from task-irrelevant regions (here: visual and ipsilateral  
371 somatosensory cortices) to task-relevant ones (contralateral somatosensory cortex).

372 To our knowledge, only two previous studies investigated the interaction between eye-closure  
373 induced and task-related alpha modulations. Both studies, using auditory paradigms without a  
374 spatial component, reported an eye-closure related increase in alpha power (Bastarrika-Iriarte &

375 Caballero-Gaudes, 2019; Wöstmann et al., 2020). Wöstmann et al. (2020) found that eye closure  
376 enhances the attentional modulation of alpha power, and Bastarrika-Iriarte & Caballero-Gaudes  
377 (2019) found that eye closure enhances the event-related alpha power increase. Neither study  
378 found an effect of eye closure on performance (i.e., accuracy). In their study, Wöstmann et al.  
379 (2020) presented to-be-attended and to-be-ignored speech streams binaurally, i.e., attention was  
380 equally distributed across auditory cortices. Importantly, they found that eye closure enhances  
381 attentional modulation primarily in non-auditory (task-irrelevant) parieto-occipital regions. This  
382 mirrors our finding that eye closure only impacts anticipatory visual (task-irrelevant) alpha  
383 modulation. Note that since somatosensory demands are equivalent across eye conditions, and any  
384 non-lateralized effects are subtracted out in our lateralization index, it follows that anticipatory  
385 somatosensory alpha remains unaffected by eye closure.

386 We found that both absolute and anticipatory visual alpha increase were associated with faster and  
387 more accurate responses in both eye conditions. This aligns with our previous findings in the  
388 somatosensory (Haegens et al., 2010, 2012) and the auditory domains (e.g., ElShafei et al., 2018),  
389 demonstrating that in non-visual tasks, visual alpha increase facilitates behavioral performance. In  
390 addition, we found that anticipatory somatosensory lateralization was associated with faster  
391 responses, regardless of eye condition. The absence of an effect of somatosensory lateralization on  
392 accuracy contradicts our previous findings that lateralization leads to better accuracy (Haegens et  
393 al., 2011; Haegens et al., 2012). However, a key difference with our current study is the presence of  
394 distracting (competing) tactile stimuli in our previous work. If alpha controls inhibition, it is  
395 conceivable that the link between somatosensory lateralization and accuracy is to a degree  
396 dependent on the presence of distracting somatosensory stimuli that require suppressing, and we  
397 may therefore not have been as sensitive to such effects here.

398 Critically, all observed alpha-performance correlations were independent of eye-closure condition;  
399 i.e., eye closure did not impact the relationship between alpha dynamics and behavioral  
400 performance. Furthermore, both global and anticipatory visual alpha changes showed similar  
401 relationships with task performance, suggesting a general (functional inhibitory) role for alpha,  
402 regardless of driving/modulatory factor behind the observed alpha dynamics. We propose that  
403 posterior alpha reflects the inhibition of task-irrelevant visual processing, and that in the presence  
404 of visual input (eyes-open condition) an increase in visual alpha power is required to achieve this,  
405 while in the absence of visual input (eyes-closed condition), visual alpha power is already elevated,  
406 hence reducing the need for additional anticipatory modulation (Figure 7).

## 407 **Conclusion**

408 The present study dissociates for the first time eye-closure induced alpha and anticipatory alpha  
409 modulations in the somatosensory domain. We demonstrate that while eye closure boosts global  
410 alpha power, it dampens anticipatory visual alpha modulation with no impact on somatosensory  
411 lateralization. Finally, we show that eye closure does not alter the impact of alpha dynamics on  
412 behavioral performance. Combined, this suggests there is an optimal posterior alpha level for  
413 somatosensory task performance, which can be achieved both through eye closure and top-down  
414 anticipatory attention. Our findings provide further support for a general inhibitory or gating role  
415 for the alpha rhythm.

416

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564

## 565 Legends

### 566 **Figure 1. Experimental paradigm and behavioral results.**

567 [A] Participants performed a tactile stimulus discrimination task where a 100% valid auditory cue  
568 directed attention either to their right or left hand in an eyes-open (EO) and an eyes-closed (EC)  
569 condition. Participants had to discriminate between two target frequencies, presented as electrical  
570 pulse trains to the cued thumb. [B] Accuracy (left panel) and reaction time (right) for the EO and EC  
571 conditions. Behavioral performance was significantly worse when participants had their eyes closed  
572 both in terms of lower accuracy and slower RT. \* $p < 0.05$ ; \*\* $p < .01$ ; \*\*\* $p < .001$ .

### 573 **Figure 2. Impact of eye closure on global power.**

574 [A] Average absolute occipital power (1–13 Hz) during the pre-stimulus window ( $t = -1$  to  $0$  s) for  
575 the EC (green) and EO (orange) conditions (shading reflects between-participant SEM). Alpha power  
576 was significantly higher in the EC condition compared to the EO condition. Grey bars indicate  
577 significant differences between conditions. [B] Topography of significant (masked at  $p < 0.05$ )  
578 cluster t-values for the alpha band for EO vs. EC (as marked in A) on sensor level (left panel) and  
579 power distribution of these differences in source space (right). [C] Same as panel A for 13–30 Hz.  
580 Beta power was significantly higher in the EC condition compared to the EO condition. [D] Same as  
581 panel B for the beta band (as marked in C).

### 582 **Figure 3. Impact of eye closure on anticipatory visual alpha modulation.**

583 [A] Topography of the normalized pre-stimulus alpha power modulation for the attention-left  
584 condition (i.e., pre-stimulus window vs. baseline) for EO (left panel) and EC (right). [B] Same as A for  
585 the attention-right condition. [C] Topography of significant (masked at  $p < 0.05$ ) cluster t-values for  
586 EO vs. EC for the attention-left condition on sensor level (left panel), and power distribution of

587 these differences in source space (right). [D] Same as C for the attention-right condition. [E]  
588 Normalized occipital pre-stimulus alpha power for the attention-left condition (included sensors  
589 marked in topography inset), showing significant difference between eye conditions. [F] Same as E  
590 for the attention-right condition. \* $p < 0.05$ ; \*\* $p < .01$ ; \*\*\* $p < .001$ .

591 **Figure 4. Localization differences between eye-closure and anticipatory alpha modulations.**

592 [A] Distribution of the eye-closure (in blue, left) and anticipatory (in red, right) alpha modulations in  
593 source space. For visualization purposes, maximas from each modulation were transposed on one  
594 hemisphere. [B] Topography of significant (masked at  $p < 0.05$ ) cluster t-values for eye closure vs.  
595 anticipatory alpha modulations. [C] Maxima coordinates along the x-axis (left), y-axis (middle) and  
596 z-axis (right). \* $p < 0.05$ ; \*\* $p < .01$ ; \*\*\* $p < .001$ .

597 **Figure 5. Impact of eye closure on somatosensory alpha lateralization.**

598 [A] Topography of the attention-left vs attention-right anticipatory alpha power modulation for the  
599 EO condition (left panel), and power distribution of this modulation in source space (right). This  
600 modulation localizes to somatomotor regions with higher alpha power in ipsilateral and lower alpha  
601 power in contralateral regions. [B] TFRs showing the lateralized power modulation in the EO  
602 condition. Left-hemispheric sensors were mirrored to combine them with the right-hemispheric  
603 sensors. [C] Same as A for the EC condition. [D] Same as B for the EC condition. [E] Pre-stimulus  
604 alpha lateralization index (included sensors marked in topography inset), showing no significant  
605 difference between eye conditions.

606 **Figure 6. Impact of eye closure on the relationship between alpha and performance.**

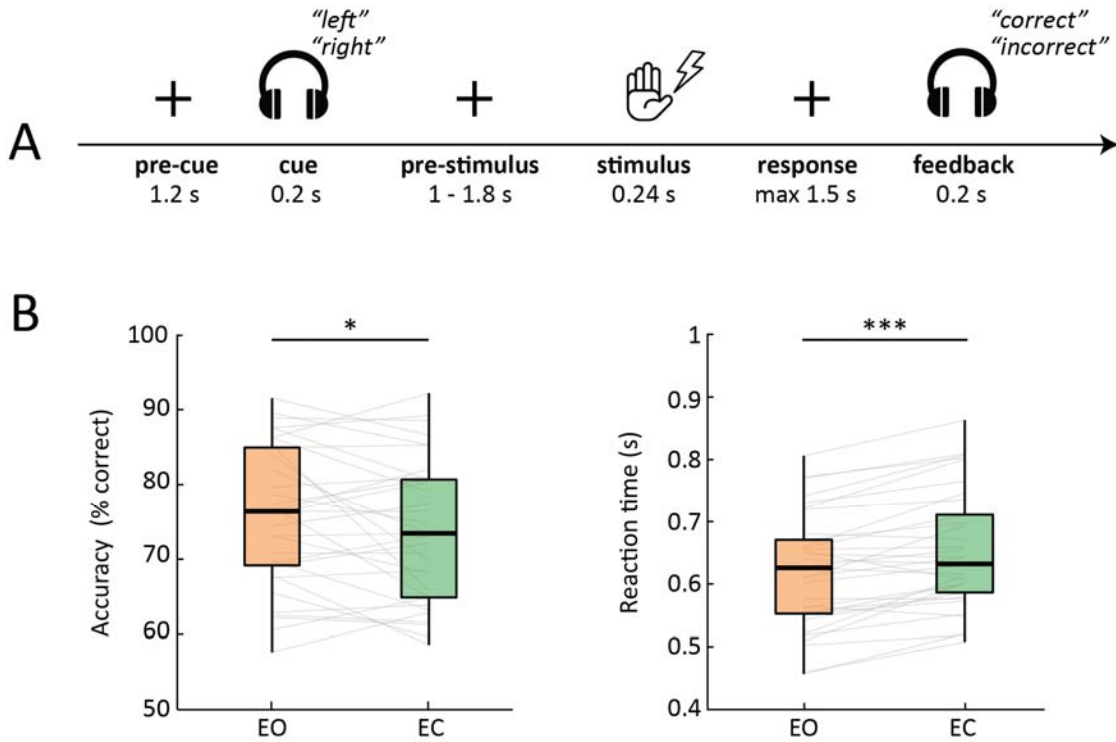
607 [A] Absolute (non-baseline corrected) pre-stimulus visual alpha power in EO (left panel) and EC  
608 (right panel) conditions for correct vs. incorrect trials. Absolute visual alpha power was higher for  
609 correct trials, regardless of eye condition. [B] Same as A for fast vs. slow trials. Absolute visual alpha

610 power was higher for fast trials, regardless of eye condition. [C] Same as A for anticipatory visual  
611 alpha modulation (baseline corrected) in EO (left panel) and EC (right panel) conditions for correct  
612 vs. incorrect trials. Anticipatory visual alpha power was higher for correct trials, regardless of eye  
613 condition. [D] Same as C for fast vs. slow trials. Anticipatory visual alpha power was higher for fast  
614 trials, regardless of eye condition. [E] Same as C for somatosensory alpha lateralization index. No  
615 significant differences were found between conditions. [F] Same as E for fast vs. slow trials.  
616 Somatosensory alpha lateralization was higher for fast trials, regardless of eye condition. \* $p < 0.05$ ;  
617 \*\* $p < .01$ ; \*\*\* $p < .001$ .

618 **Figure 7. Information gating and eye closure.**

619 In the EO baseline interval, information processing is equivalent across task-relevant  
620 somatosensory and task-irrelevant visual regions. Thus, in the pre-stimulus interval anticipatory  
621 modulation drives alpha levels to the optimal gating threshold at which information flow is gated  
622 away from visual regions by inhibiting the processing of visual input. In the EC baseline interval  
623 information processing is already diminished due to the absence of visual input. However, alpha  
624 level has not yet reached the optimal threshold to entirely gate information flow. Thus, in the pre-  
625 stimulus interval, alpha level is further heightened to reach the gating threshold and thus inhibiting  
626 information processing in visual regions.

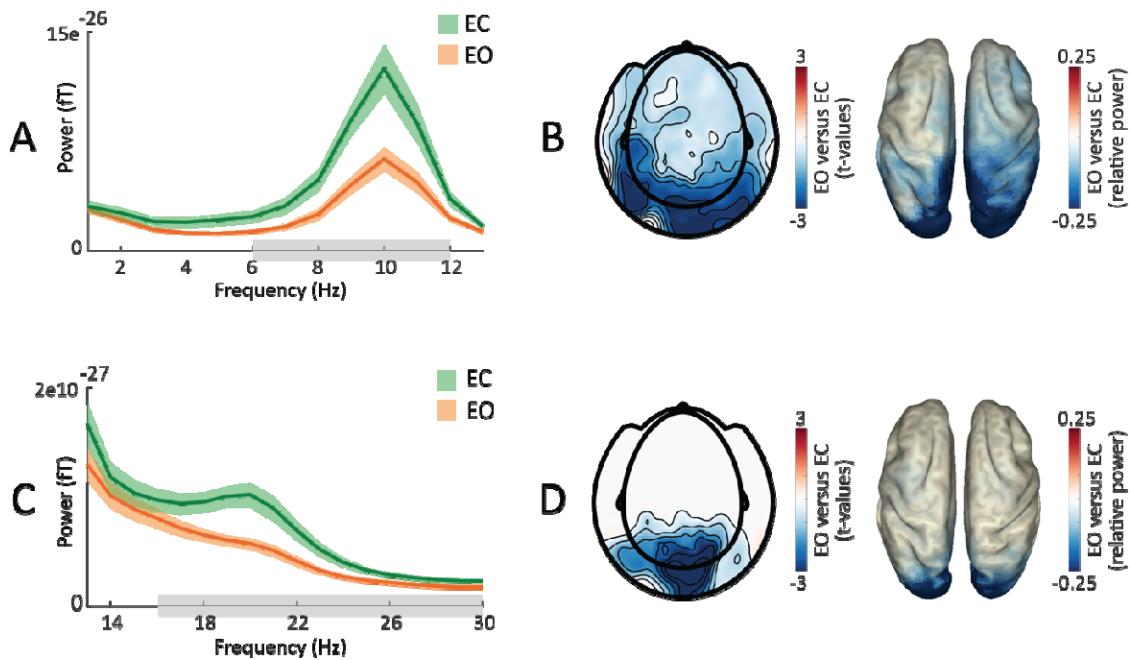
627 Figures



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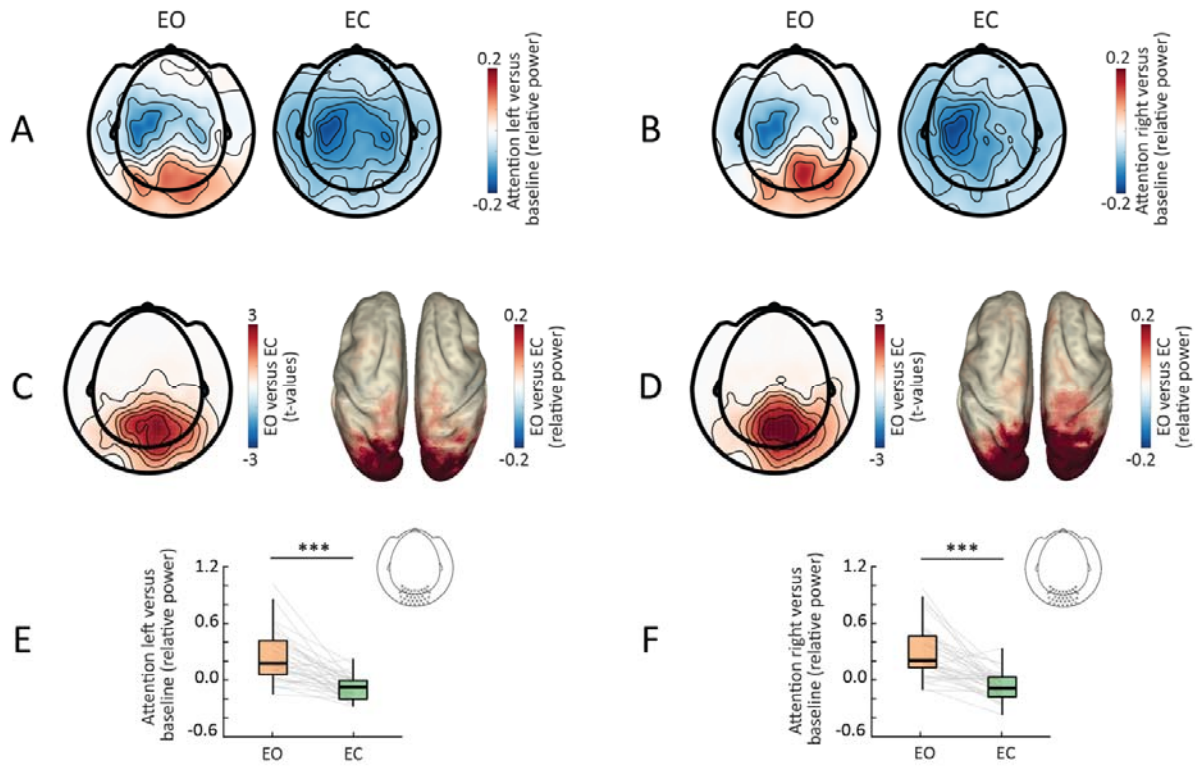
Figure 1



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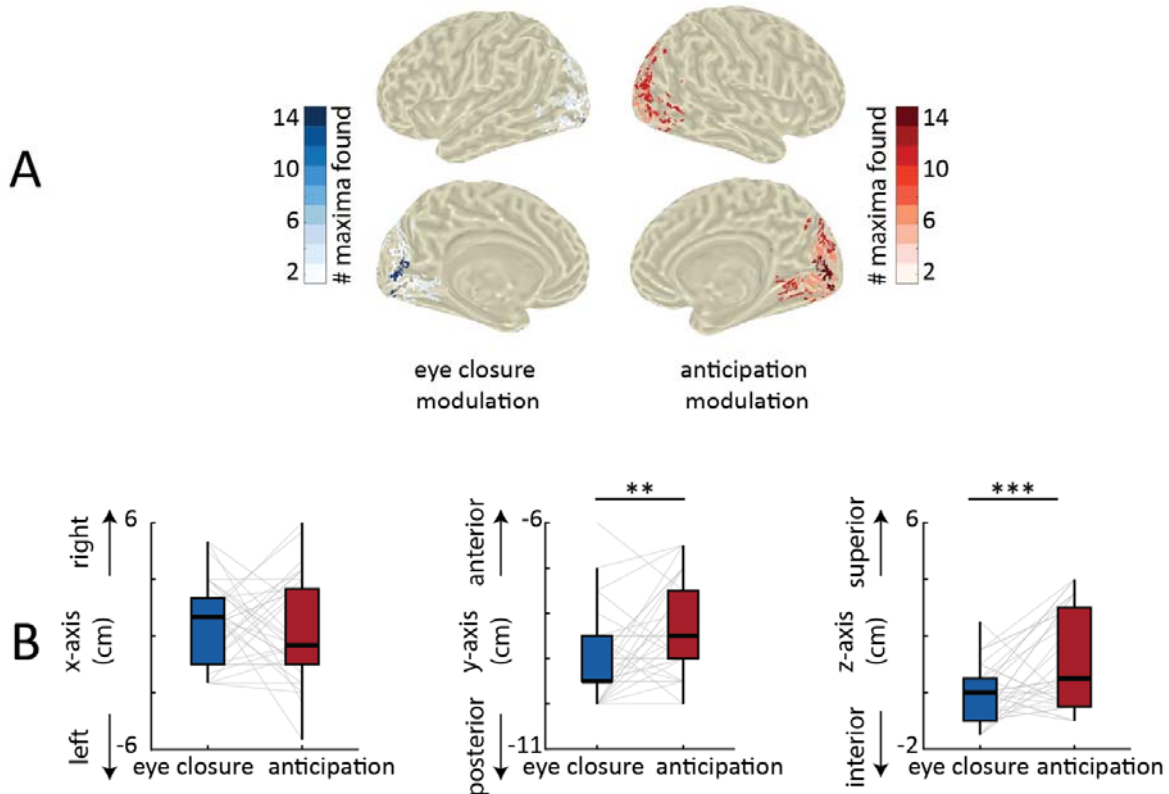
Figure 2



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Figure 3



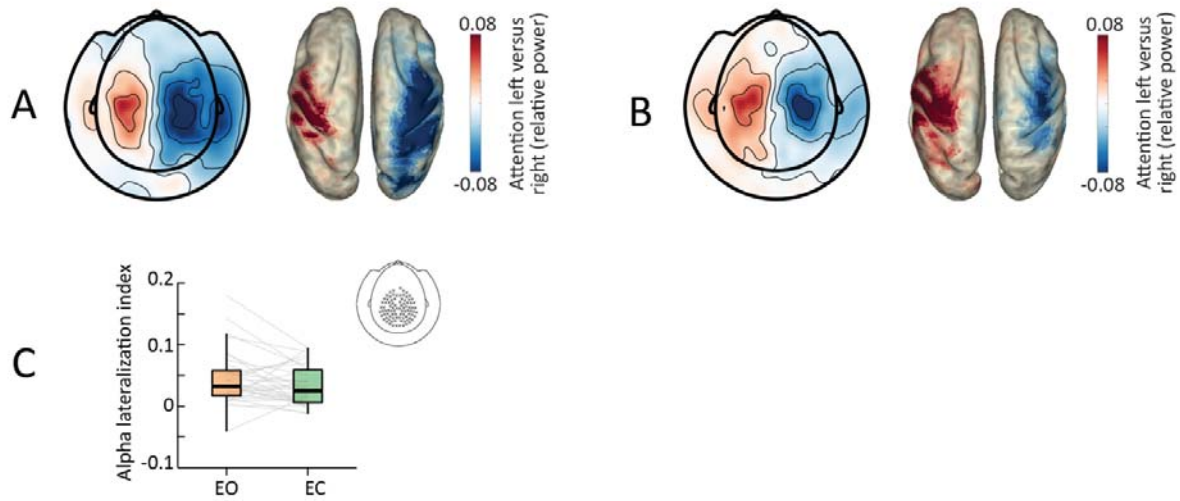
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Figure 4



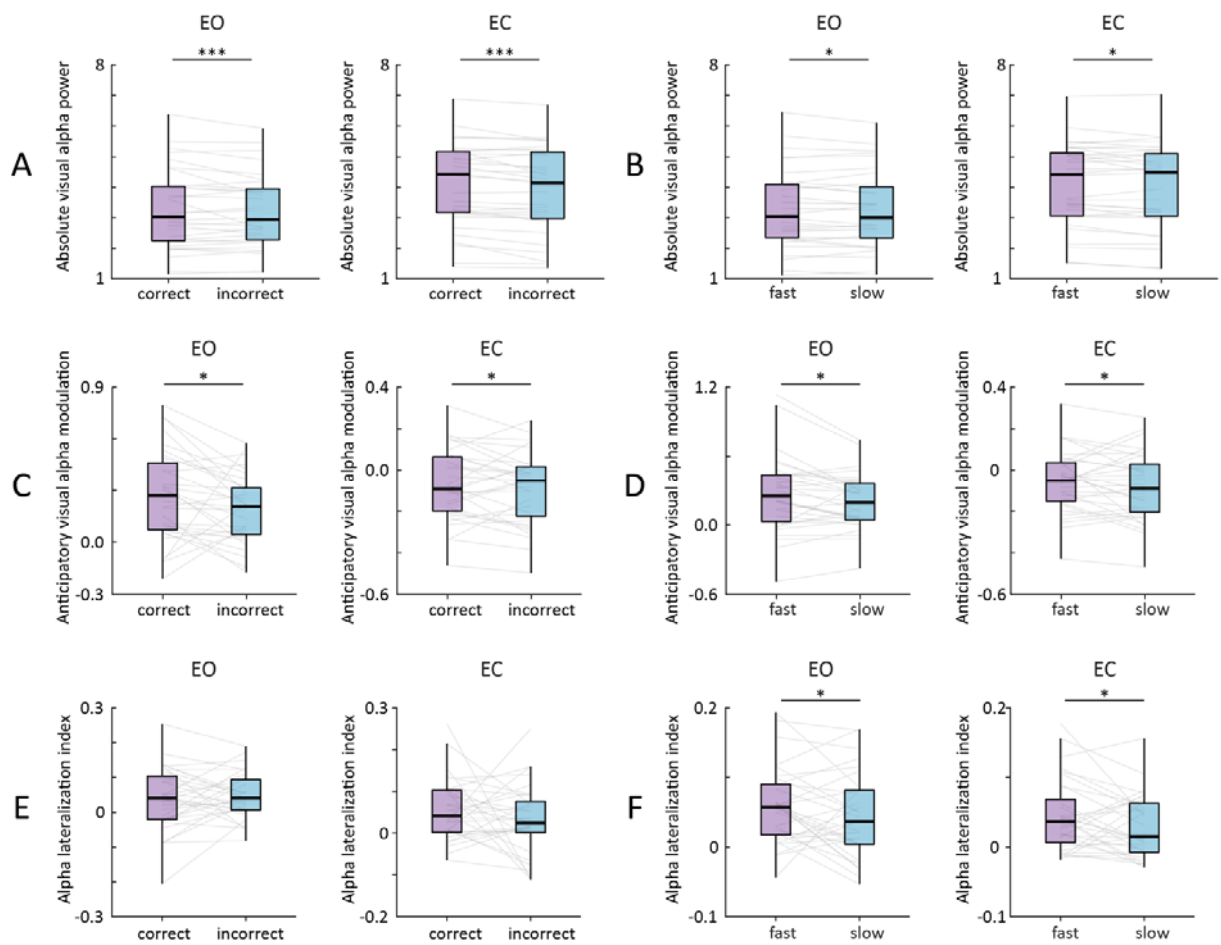




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Figure 5

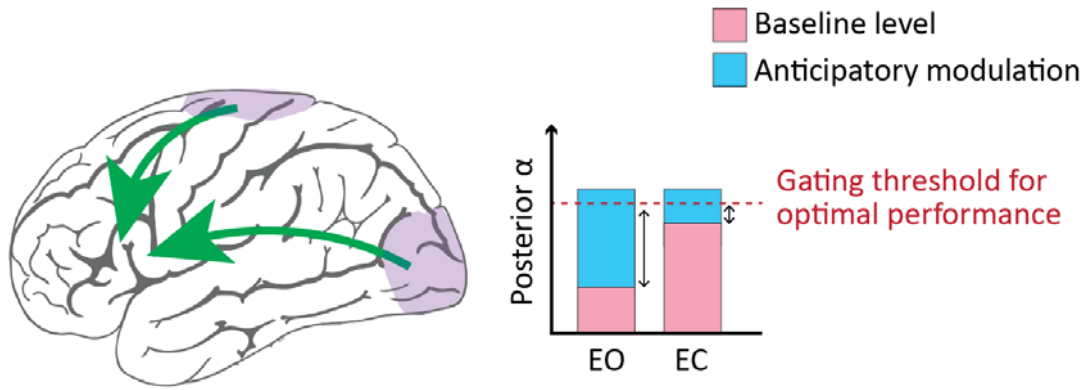


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Figure 6



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Figure 7