
Research Article: New Research | Cognition and Behavior

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

<https://doi.org/10.1523/ENEURO.0412-21.2021>

Cite as: eNeuro 2021; 10.1523/ENEURO.0412-21.2021

Received: 1 October 2021

Revised: 25 November 2021

Accepted: 1 December 2021

This Early Release article has been peer-reviewed and accepted, but has not been through the composition and copyediting processes. The final version may differ slightly in style or formatting and will contain links to any extended data.

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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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15 **Number of pages:** 34

16 **Number of figures:** 7, **tables:** 0, **multimedia:** 0, **and 3D models:** 0

17 **Number of words for abstract:** 214, **introduction:** 553, **and discussion:** 1128

18 **Conflict of interest statement**

19 The authors declare that the research was conducted in the absence of any commercial or financial
20 relationships that could be construed as a potential conflict of interest.

21 **Funding sources**

22 This work was supported by the Netherlands Organization for Scientific Research Vidi grant
23 016.Vidi.185.137.

24

25 Abstract

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

43

44 Significance Statement

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

54

55 Introduction

56 Since the discovery of the cortical alpha rhythm by Hans Berger (1929) almost a century ago, it has
57 been known that a general increase of posterior (visual) alpha power occurs when awake
58 participants close their eyes (Adrian & Matthews, 1934). While traditionally the alpha rhythm was
59 associated with a state of cortical idling (Pfurtscheller et al., 1996), more recent work suggests that
60 alpha activity reflects a mechanism of functional inhibition (Foxe & Snyder, 2011; Haegens et al.,
61 2011; Jensen & Mazaheri, 2010; Klimesch et al., 2007). In support of such an inhibitory mechanism,
62 visual spatial attention is known to modulate alpha activity in a lateralized fashion: alpha decreases
63 contralateral to the attended location (Sauseng et al., 2005) and increases contralateral to the
64 ignored location, presumably to suppress distracting input (Kelly et al., 2009; Worden et al., 2000;
65 Wöstmann et al., 2019). This lateralized alpha activity correlates with visual detection performance
66 (Händel et al., 2011; Thut et al., 2006). Similar patterns have been observed for the auditory
67 (Banerjee et al., 2011; Frey et al., 2014; Straub et al., 2014; Wöstmann et al., 2016) and
68 somatosensory domains (Anderson & Ding, 2011; Haegens et al., 2011, 2012; Jones et al., 2010).

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

77 induced alpha increase relates to alpha lateralization patterns observed in the context of spatial
78 attention.

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

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

98

99 Materials and Methods

100 Participants

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

107 Experimental design

108 Participants performed a tactile discrimination task (Figure 1; task adapted from Haegens et al.,
109 2011) while their brain activity was recorded using MEG. Participants received an electrical stimulus
110 (pulse train of a low or high frequency) to either the right or left thumb. Participants were
111 instructed to determine as fast and accurately as possible whether the perceived stimulus was of
112 low or high frequency, responding via button press with their right index finger (left button press
113 indicated the low frequency; right button press indicated the high frequency). Prior to the stimulus
114 presentation, an auditory cue (verbal “right” or “left”) directed participants’ attention to either
115 their right or left hand. Spatial cues were always valid. Each trial started with a pre-cue interval of
116 1.2 s followed by the auditory cue (0.2 s), a jittered 1–1.8 s pre-stimulus interval, the tactile
117 stimulus (0.24-s pulse train), a response window of maximum 1.5 s, and finally auditory feedback
118 indicating whether the answer was correct or incorrect.

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

121 condition with 76 trials each, resulting in a total of 304 trials per condition. During the EO condition,
122 participants were instructed to fixate on a fixation cross in the middle of the screen. For the EC
123 condition, participants kept their eyes closed for the duration of the block. After each block,
124 participants were presented with a short questionnaire to rate their sleepiness level (very sleepy,
125 sleepy, awake, very awake). This was done in order to check for potential confound of decreased
126 arousal with eye closure. Prior to the experiment, participants performed four training blocks (two
127 per condition, 12 trials per block), during which they were familiarized with the task.

128 Stimulus presentation

129 We used the same setup as in Haegens et al. (2011): Electrical stimuli were delivered with two
130 constant-current high-voltage stimulators (Digitimer Ltd, Model DS7A) to the right and left thumb.
131 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
132 electric pulses was set to 150% of the participant's sensory threshold level. This level was
133 established during a practice session before the recordings, for each thumb independently. Low
134 (either 25 or 33.3 Hz) and high frequencies (41.7, 50, or 66.7 Hz) were determined for each
135 participant individually to ensure successful execution of the task, above chance level but below
136 ceiling performance. Auditory cues and feedback (0.2-s length each) were computer-generated and
137 presented binaurally through air-conducting tubes.

138 Data acquisition

139 Whole-head MEG data were acquired at a sampling frequency of 1200 Hz with a 275-channel MEG
140 system with axial gradiometers (CTF MEG Systems, VSM MedTech Ltd.) in a dimly lit magnetically
141 shielded room. Six permanently faulty channels were disabled during the recordings, leaving 269
142 recorded MEG channels. Three fiducial coils were placed at the participant's nasion and both ear
143 canals, to provide online monitoring of participant's head position (Stolk et al., 2013) and offline

144 anatomical landmarks for co-registration. Eye position was recorded using an eye tracker (EyeLink,
145 SR Research Ltd.). Upon completion of the MEG session, participant's head shape and the location
146 of the three fiducial coils were digitized using a Polhemus 3D tracking device (Polhemus, Colchester,
147 Vermont, United States). Anatomical T1-weighted MRIs were obtained during a separate session.
148 To improve co-registration of the MRIs and MEG data, earplugs with a drop of Vitamin E were
149 placed at participant's ear canals during MRI acquisition. These anatomical scans were used for
150 source reconstruction of the MEG signal.

151 Pre-processing

152 MEG data were preprocessed offline and analyzed using the FieldTrip toolbox (Oostenveld et al.,
153 2011) and custom-built MATLAB scripts. The MEG signal was epoched based on the onset of the
154 somatosensory stimulus ($t = -4$ to 3 s). The data were downsampled to a sampling frequency of 300
155 Hz, after applying a notch filter to remove line noise and harmonics (50, 100, and 150 Hz). Bad
156 channels and trials were rejected via visual inspection before independent component analysis
157 (Jung et al., 2001) was applied. Subsequently, components representing eye-related and heart-
158 related artefacts were projected out of the data (on average, eight components were removed per
159 participant). Finally, for the resulting data, outlier trials of extreme variance (higher than 2 standard
160 deviations) were removed. This resulted in an average of 537 (± 7 SEM) trials and 268 channels per
161 participant for the reported analyses.

162 Spectral analysis

163 First, we calculated the planar representation of the MEG field distribution from the single-trial
164 data using the nearest-neighbor method. This transformation makes interpretation of the sensor-
165 level data easier as the signal amplitude is typically maximal above a source. Next, we computed
166 spectral representations for two 1-s time windows: the pre-stimulus window and the pre-cue

167 window (i.e., baseline), aligned to stimulus and cue onset, respectively. Each window was
168 multiplied with a Hanning taper, and power spectra (1–30 Hz; 1-Hz resolution) were computed
169 using a fast Fourier transform (FFT) approach. Additionally, for a time-resolved-representation of
170 the spectral power distribution, we computed time-frequency representations (TFRs) of the power
171 spectra for the full trials per experimental condition. To this end we used an adaptive sliding time
172 window of five cycles length per frequency ($\Delta t = 5/f$; 20-ms step size).

173 Alpha peak frequency

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

185 Statistical analysis

186 In order to investigate whether power differences between the EO and the EC conditions were
187 significant, we used nonparametric cluster-based permutation tests (Maris & Oostenveld, 2007). In
188 brief, this test first calculates paired t-tests for each sensor at each time and/or frequency point,
189 which are then thresholded at $p < 0.05$ and clustered on the basis of spatial, temporal, and/or

190 spectral adjacency. The sum of t-values within each cluster is retained, and the procedure is
191 repeated 1000 times on permuted data in which the condition assignment within each individual is
192 randomized. On each permutation, the maximum sum is retained. Across all permutations, this
193 yields a distribution of 1000 maximum cluster values. From this distribution, the probability of each
194 empirically observed cluster statistic can be derived (evaluated at $\alpha = 0.05$).

195 We used this permutation test to investigate the impact of eye closure on (i) overall oscillatory
196 power, by contrasting power in the pre-stimulus interval between eye conditions, (ii) anticipatory
197 visual alpha activity, by contrasting pre-stimulus baseline-normalized power between eye
198 conditions, for each cue separately, and (iii) somatosensory alpha activity, by contrasting the pre-
199 stimulus attention modulation index, calculated as $(\text{attention-left} - \text{attention-right}) / (\text{attention-left}$
200 $+ \text{attention-right})$ between eye conditions.

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

210 Alpha lateralization index

211 To capture the relative pre-stimulus somatosensory alpha distribution over both hemispheres in
212 one measure, we computed a lateralization index of alpha power (Haegens et al., 2011; Thut et al.,

213 2006) for each participant, using individual somatosensory ROIs: alpha lateralization index = (alpha-
214 ipsilateral - alpha-contralateral) / (alpha-ipsilateral + alpha-contralateral). This index gives positive
215 values if alpha power is higher over the ipsilateral hemisphere and/or lower over the contralateral
216 hemisphere (with contra- and ipsilateral sides defined with respect to the spatial cue). Negative
217 values arise if alpha power activity is lower over the ipsilateral hemisphere and/or higher over the
218 contralateral hemisphere.

219 Source reconstruction

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

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

237 Results

238 Eye closure impairs performance

239 Performance over all 33 participants for both eye conditions combined was an average accuracy of
240 74.4% ($SD = 9.96\%$) and an average reaction time (correct trials only) of 0.64 s ($SD = 0.1$ s).
241 Participants were more accurate ($t(32) = 2.32$, $p = 0.023$, paired-test, mean EO = 75.7% + 9.9 SD,
242 mean EC = 73.7% \pm 9.9 SD) and faster ($t(32) = -6.8$, $p < 0.001$, mean EO = 0.62 s \pm 0.1 SD, mean EC =
243 0.65 s \pm 0.1 SD) at discriminating the frequency of the tactile stimuli in the EO condition in
244 comparison to the EC condition (Figure 1B).

245 Further, we investigated the impact of eye closure (two levels: EC and EO) and block order (four
246 levels: first, second, third and fourth) on the sleepiness score reported at the end of each block. We
247 found a main effect of eye condition ($F(1,26) = 9.7$, $p = 0.004$, ANOVA), with participants reporting
248 being more awake when they had their eyes open. In addition, we found a main effect of block
249 order ($F(3,78) = 5.32$, $p = 0.009$), with participants reporting being more awake in the first block in
250 comparison to the second ($t(26) = -3.15$, $p = 0.014$, posthoc paired t-test), third ($t(26) = -3.45$ $p =$
251 0.005) and fourth ($t(26) = -3.15$, $p = 0.014$), with no significant interaction ($F(3,78) = 1.11$, $p = 0.35$).
252 Note that differences in sleepiness scores did not correlate with differences in behavioral
253 performance between eye conditions (RT: $r(26) = -0.19$, $p = 0.32$; accuracy: $r(26) = 0.22$, $p = 0.25$).

254 Eye closure boosts widespread oscillatory activity

255 In order to investigate the impact of eye closure on overall oscillatory power, we contrasted power
256 spectra (1–30 Hz) during the pre-stimulus window between the EO and the EC conditions (Figure 2).
257 We found that power was higher for EC than EO (cluster-corrected $p < 0.001$), both in the alpha (6–
258 12 Hz) and in the beta range (17–30 Hz). The alpha cluster was widespread with a spectral peak at

259 10 Hz, while the beta cluster was concentrated towards posterior sensors, showing the highest
260 difference between conditions around 20 Hz. While in this study we focused on alpha activity, as a
261 control we compared event-related fields (ERFs) between eye conditions and found no differences
262 (cluster-corrected $p > 0.5$; test included all sensors, $t = 0$ to 0.6 s).

263 Eye closure impacts anticipatory visual alpha modulation

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

277 Eye-closure related and anticipatory alpha modulations are spatially distinct

278 To address the question of whether eye-closure induced modulations and anticipatory alpha
279 modulations share the same underlying cortical generators (i.e., localize to the same cortical
280 regions), we compared the maxima of these effects in source space. For each participant, we
281 identified the voxel displaying the maximal difference in absolute alpha power in the EO and the EC

282 conditions, and the voxel displaying the maximal anticipatory pre-stimulus alpha power
283 modulation. We then contrasted the x- y- and z- coordinates of these maxima using paired t-tests.
284 We found that maxima differed in their distribution along the y-axis ($t(32) = -2.83$, $p = 0.007$ paired
285 t-test) and the z-axis ($t(32) = -3.7$, $p < 0.001$). In other words, maxima of the anticipatory alpha
286 modulations were located more anterior and superior in comparison to the eye-closure induced
287 modulations (Figure 4), with no differences in the distribution along the x-axis (i.e., left vs. right;
288 $t(32) = 0.36$, $p = 0.71$). While this points to distinct cortical generators for eye-closure and
289 anticipatory alpha modulations, we are cognizant of the inherent limitation of MEG source
290 localization as well as inter-individual variability and anatomical differences across participants;
291 invasive techniques might be required to conclusively resolve this matter.

292 Eye closure does not impact somatosensory alpha modulation

293 In order to investigate how eye closure impacts anticipatory somatosensory alpha modulation, we
294 contrasted the pre-stimulus attention modulation index (calculated as (attention-left - attention-
295 right) / (attention-left + attention-right)) between EO and EC conditions. While there was a
296 significant attention modulation—i.e., a pattern of lateralized sensorimotor alpha power (left
297 increase $p = 0.007$; right decrease $p < 0.001$) when contrasting left vs. right attention conditions—
298 no significant differences were found between eye conditions ($p = 0.34$; Figure 5). Thus, while both
299 overall and anticipatory visual alpha activity differed between eye conditions, anticipatory
300 somatosensory alpha modulation was not affected by eye closure.

301 Eye closure does not impact the link between anticipatory alpha and behavioral performance

302 Finally, we investigated the impact of eye closure on the link between pre-stimulus alpha
303 modulation and behavioral performance. First, we analyzed the relationship between pre-stimulus
304 visual alpha power, both absolute (non-baseline normalized) and anticipatory (baseline-normalized)

305 modulations, and performance, by binning the data based on correct vs. incorrect responses, and
306 fast vs. slow RTs (divided by a median split).

307 For absolute visual alpha power and accuracy (Figure 6A), we found a significant main effect of
308 accuracy ($F(1, 31) = 15.2, p < 0.001$, ANOVA) with absolute visual alpha power being higher in
309 correct trials in comparison to incorrect trials. In addition, we found a significant main effect of eye
310 condition ($F(1, 31) = 26.92, p < 0.001$) and no significant interaction between eye condition and
311 accuracy ($F(1, 31) = 1.15, p = 0.29$). For absolute visual alpha power and RT (Figure 6B), we found a
312 significant main effect of RT ($F(1, 31) = 6.11, p = 0.02$, ANOVA) with absolute visual alpha power
313 being higher in fast trials in comparison to slow trials. In addition, we found a significant main effect
314 of eye condition ($F(1, 31) = 31.53, p < 0.001$) and no significant interaction between eye condition
315 and RT ($F(1, 31) = 0.65, p = 0.42$). In sum, absolute visual alpha power predicted more accurate and
316 faster responses, regardless of eye condition.

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

327 For somatosensory alpha lateralization and accuracy (Figure 6E), we did not find a significant main
328 effect of accuracy ($F(1, 31) = 0.39, p = 0.53$, ANOVA) nor a significant main effect of eye condition
329 ($F(1, 31) = 0.001, p = 0.98$), nor a significant interaction between eye condition and accuracy ($F(1,$
330 $31) = 1.19, p = 0.28$). For somatosensory alpha lateralization and RT (Figure 6F), we found a
331 significant main effect of RT ($F(1, 31) = 5.31, p = 0.027$, ANOVA) with somatosensory alpha
332 lateralization being higher for faster trials. We found neither a significant main effect of eye
333 condition ($F(1, 31) = 2.47, p = 0.12$) nor a significant interaction between eye condition and RT (F
334 $(1, 31) = 0.001, p = 0.98$). In sum, somatosensory alpha lateralization predicted faster responses,
335 regardless of eye condition.

336

337 Discussion

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

346 Eye closure impacts overall state

347 Participants were less accurate and slower to discriminate tactile stimuli when their eyes were
348 closed. While there have been several reports of a positive impact of eye closure on performance
349 (e.g., perceptual sensitivity: Brodoehl, Klingner, Stieglitz, et al., 2015; memory retrieval: Parker &
350 Dagnall, 2020; Vredeveldt et al., 2011), other studies have reported no effects (e.g., memory
351 retrieval: Bastarrika-Iriarte & Caballero-Gaudes, 2019; selective attention: Wöstmann et al., 2020)
352 or negative impact (somatosensory discrimination Götz et al., 2017). Differences in paradigms
353 (attention versus memory) and sensory modalities (auditory versus somatosensory) between these
354 various reports renders it difficult to define common factors that govern the interaction between
355 eye closure and behavioral performance. Nevertheless, Götz et al. (2017) argue that for tactile
356 perception, eye closure might boost sensitivity but hinder discriminability, possibly due to the
357 dependence of tactile discriminability upon extrastriate visual processing (Sathian & Zangaladze,
358 2002). Following this logic, in our tactile discrimination task eye closure diminishes extrastriate
359 visual processing, leading to worse behavioral performance.

360 Simultaneous with this behavioral deterioration, and as has been long known (e.g., Adrian &
361 Matthews, 1934; Geller et al., 2014; Wöstmann et al., 2020), alpha power increased with eye
362 closure. This increase was widespread, extending beyond occipital regions, and additionally
363 included frequency ranges neighboring the alpha band (i.e., theta and beta). This observation
364 supports the idea that eye closure does not only reflect a disengagement of visual areas, but rather
365 a cortical state transition (Barry et al., 2007; Harris & Thiele, 2011; Marx et al., 2004). One
366 interesting question is whether the observed oscillatory shifts are dependent on (lack of) light input
367 or eye closure per se. Findings from resting state studies have been contradictory, with reports that
368 alpha power is modulated by light input but not eye closure itself, and vice versa (Ben-Simon et al.,
369 2013; Jao et al., 2013). Future research should investigate how light input impacts the interaction
370 between eye closure and oscillatory dynamics during active tasks.

371 Eye closure versus anticipatory attention

372 Although eye closure led to a general increase of alpha power, we found a significant reduction of
373 *anticipatory* visual alpha modulation in comparison to the eyes-open condition, with the maxima of
374 this latter phenomenon extending more anterior than the widespread alpha increase.
375 Somatosensory alpha lateralization was not affected by eye closure. These observed alpha
376 modulations are in line with the proposal that alpha power reflects a functional mechanism of
377 inhibition (Foxe & Snyder, 2011; Haegens et al., 2011; Jensen & Mazaheri, 2010; Klimesch et al.,
378 2007) that regulates cortical excitability to gate information from task-irrelevant regions (here:
379 visual and ipsilateral somatosensory cortices) to task-relevant ones (contralateral somatosensory
380 cortex).

381 To our knowledge, only two previous studies investigated the interaction between eye-closure
382 induced and task-related alpha modulations. Both studies, using auditory paradigms without a

383 spatial component, reported an eye-closure related increase in alpha power (Bastarrika-Iriarte &
384 Caballero-Gaudes, 2019; Wöstmann et al., 2020). Wöstmann et al. (2020) found that eye closure
385 enhances the attentional modulation of alpha power, and Bastarrika-Iriarte & Caballero-Gaudes
386 (2019) found that eye closure enhances the event-related alpha power increase. Neither study
387 found an effect of eye closure on performance (i.e., accuracy). In their study, Wöstmann et al.
388 (2020) presented to-be-attended and to-be-ignored speech streams binaurally, i.e., attention was
389 equally distributed across auditory cortices. Importantly, they found that eye closure enhances
390 attentional modulation primarily in non-auditory (task-irrelevant) parieto-occipital regions. This
391 mirrors our finding that eye closure only impacts anticipatory visual (task-irrelevant) alpha
392 modulation. Note that since somatosensory demands are equivalent across eye conditions, and any
393 non-lateralized effects are subtracted out in our lateralization index, it follows that anticipatory
394 somatosensory alpha remains unaffected by eye closure.

395 We found that both absolute and anticipatory visual alpha increase were associated with faster and
396 more accurate responses in both eye conditions. This aligns with our previous findings in the
397 somatosensory (Haegens et al., 2010, 2012) and the auditory domains (e.g., ElShafei et al., 2018),
398 demonstrating that in non-visual tasks, visual alpha increase facilitates behavioral performance. In
399 addition, we found that anticipatory somatosensory lateralization was associated with faster
400 responses, regardless of eye condition. The absence of an effect of somatosensory lateralization on
401 accuracy contradicts our previous findings that lateralization leads to better accuracy (Haegens et
402 al., 2011; Haegens et al., 2012). However, a key difference with our current study is the presence of
403 distracting (competing) tactile stimuli in our previous work. If alpha controls inhibition, it is
404 conceivable that the link between somatosensory lateralization and accuracy is to a degree

405 dependent on the presence of distracting somatosensory stimuli that require suppressing, and we
406 may therefore not have been as sensitive to such effects here.

407 Critically, all observed alpha-performance correlations were independent of eye-closure condition;
408 i.e., eye closure did not impact the relationship between alpha dynamics and behavioral
409 performance. Furthermore, both overall and anticipatory visual alpha changes showed similar
410 relationships with task performance, suggesting a general (functional inhibitory) role for alpha,
411 regardless of driving/modulatory factor behind the observed alpha dynamics. We propose that
412 visual alpha reflects the inhibition of task-irrelevant visual processing, and that in the presence of
413 visual input (eyes-open condition) an increase in visual alpha power is required to achieve this,
414 while in the absence of visual input (eyes-closed condition), visual alpha power is already elevated,
415 hence reducing the need for additional anticipatory modulation (Figure 7). This optimal visual alpha
416 level might coincide with either a plateau, i.e., a physiological maximum beyond which increases in
417 alpha levels are not possible, or the peak of an inverted U-shape relationship (between alpha and
418 performance) beyond which increases in alpha level could be detrimental.

419 Conclusion

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

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573 Legends

574 **Figure 1. Experimental paradigm and behavioral results.**

575 [A] Participants performed a tactile stimulus discrimination task where a 100% valid auditory cue
576 directed attention either to their right or left hand in an eyes-open (EO) and an eyes-closed (EC)
577 condition. Participants had to discriminate between two target frequencies, presented as electrical
578 pulse trains to the cued thumb. [B] Accuracy (left panel) and reaction time (right) for the EO and EC
579 conditions. Behavioral performance was significantly worse when participants had their eyes closed
580 both in terms of lower accuracy and slower RT. * $p < 0.05$; ** $p < .01$; *** $p < .001$. Within each boxplot,
581 the horizontal line represents the median, the box delineates the area between the first and third
582 quartiles (interquartile range).

583 **Figure 2. Impact of eye closure on overall power.**

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

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

593 [A] Topography of the normalized pre-stimulus alpha power modulation for the attention-left
594 condition (i.e., pre-stimulus window vs. baseline) for EO (left panel) and EC (right). [B] Same as A for

595 the attention-right condition. [C] Topography of significant (masked at $p < 0.05$) cluster t-values for
596 EO vs. EC for the attention-left condition on sensor level (left panel), and power distribution of
597 these differences in source space (right). [D] Same as C for the attention-right condition. [E]
598 Normalized occipital pre-stimulus alpha power for the attention-left condition (included sensors
599 marked in topography inset), showing significant difference between eye conditions. [F] Same as E
600 for the attention-right condition. * $p < 0.05$; ** $p < .01$; *** $p < .001$.

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

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

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

608 [A] Topography of the attention-left vs attention-right anticipatory alpha power modulation for the
609 EO condition (left panel), and power distribution of this modulation in source space (right). This
610 modulation localizes to somatomotor regions with higher alpha power in ipsilateral and lower alpha
611 power in contralateral regions. [B] Same as A for the EC condition. [C] Pre-stimulus alpha
612 lateralization index (included sensors marked in topography inset), showing no significant
613 difference between eye conditions.

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

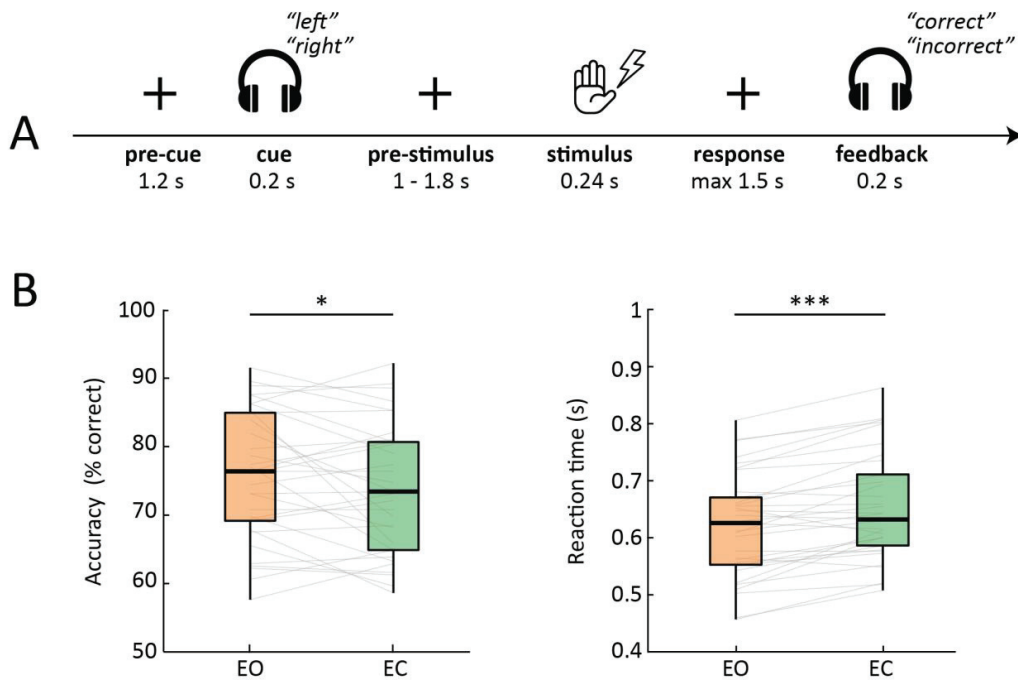
615 [A] Absolute (non-baseline corrected) pre-stimulus visual alpha power in EO (left panel) and EC
616 (right panel) conditions for correct vs. incorrect trials. Absolute visual alpha power was higher for
617 correct trials, regardless of eye condition. [B] Same as A for fast vs. slow trials. Absolute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

618 power was higher for fast trials, regardless of eye condition. [C] Same as A for anticipatory visual
619 alpha modulation (baseline corrected) in EO (left panel) and EC (right panel) conditions for correct
620 vs. incorrect trials. Anticipatory visual alpha power was higher for correct trials, regardless of eye
621 condition. [D] Same as C for fast vs. slow trials. Anticipatory visual alpha power was higher for fast
622 trials, regardless of eye condition. [E] Same as C for somatosensory alpha lateralization index. No
623 significant differences were found between conditions. [F] Same as E for fast vs. slow trials.
624 Somatosensory alpha lateralization was higher for fast trials, regardless of eye condition. * $p < 0.05$;
625 ** $p < .01$; *** $p < .001$.

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

627 In the EO baseline interval, information processing is equivalent across task-relevant
628 somatosensory and task-irrelevant visual regions. Thus, in the pre-stimulus interval anticipatory
629 modulation drives alpha levels to the optimal gating threshold at which information flow is gated
630 away from visual regions by inhibiting the processing of visual input. In the EC baseline interval
631 information processing is already diminished due to the absence of visual input. However, alpha
632 level has not yet reached the optimal threshold to entirely gate information flow. Thus, in the pre-
633 stimulus interval, alpha level is further heightened to reach the gating threshold and thus inhibiting
634 information processing in visual regions. Please note green arrows indicate general information
635 flow rather than information flow to a certain region.

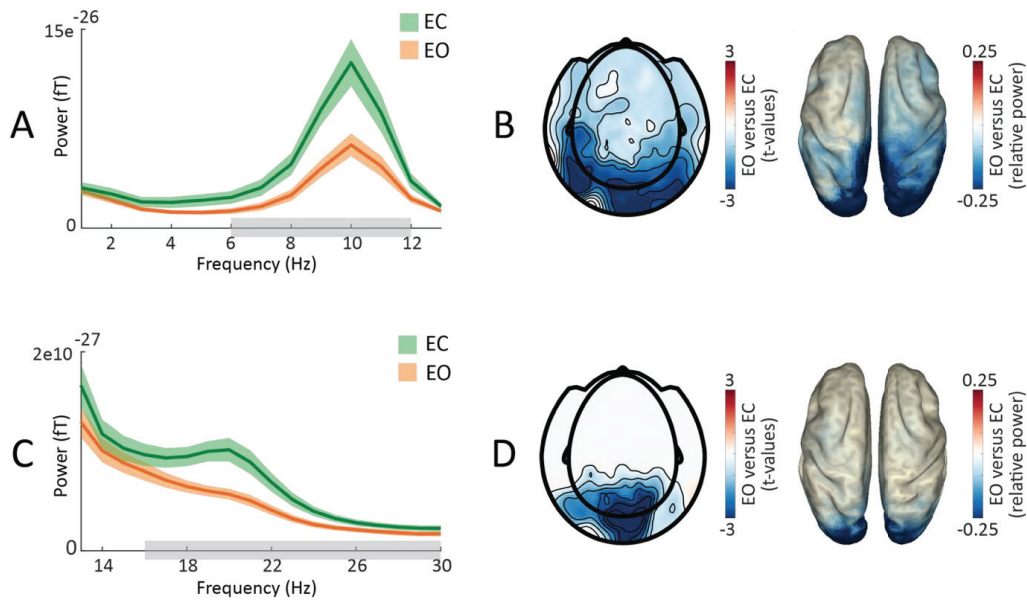
636 Figures



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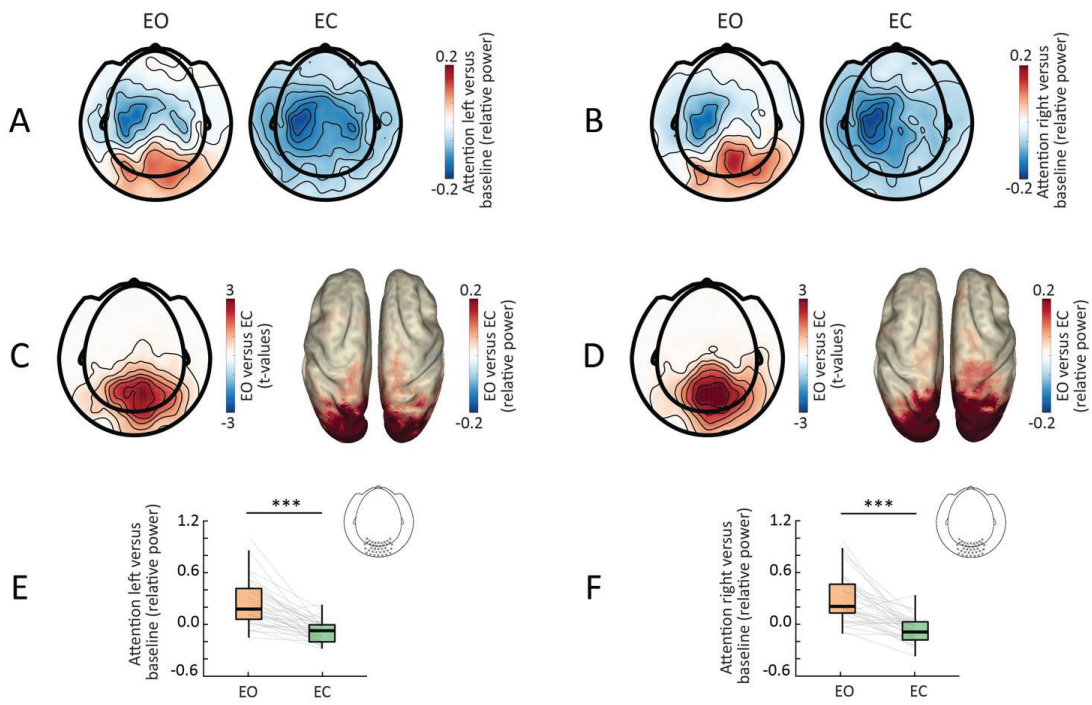
Figure 1



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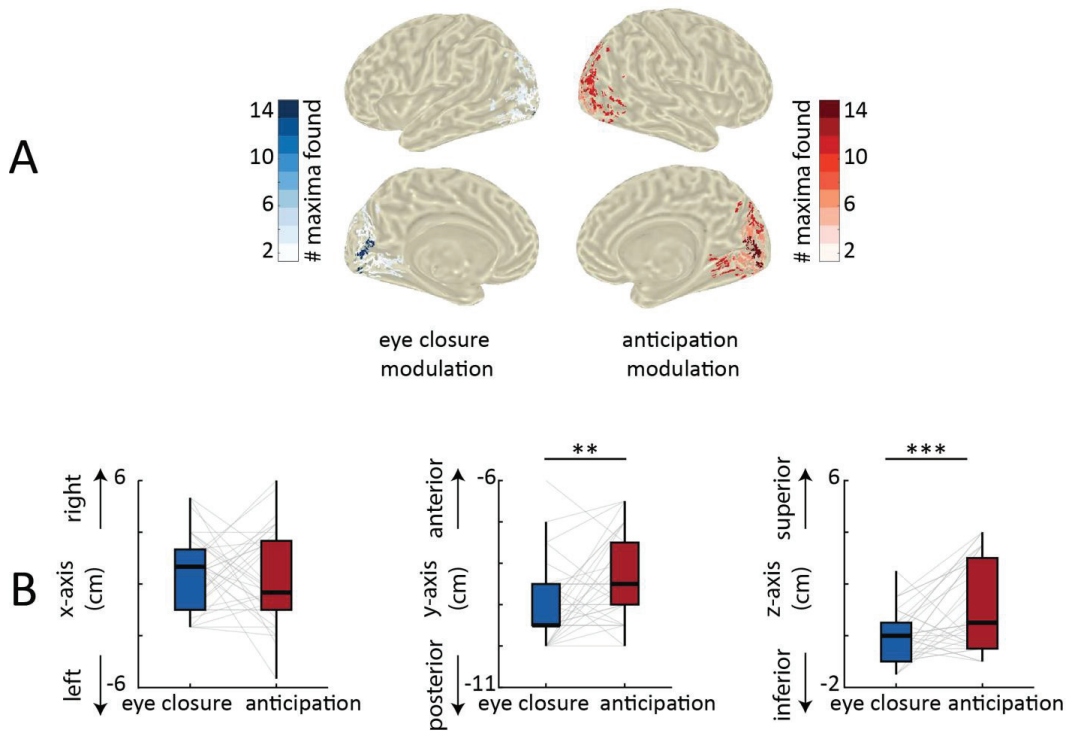
Figure 2



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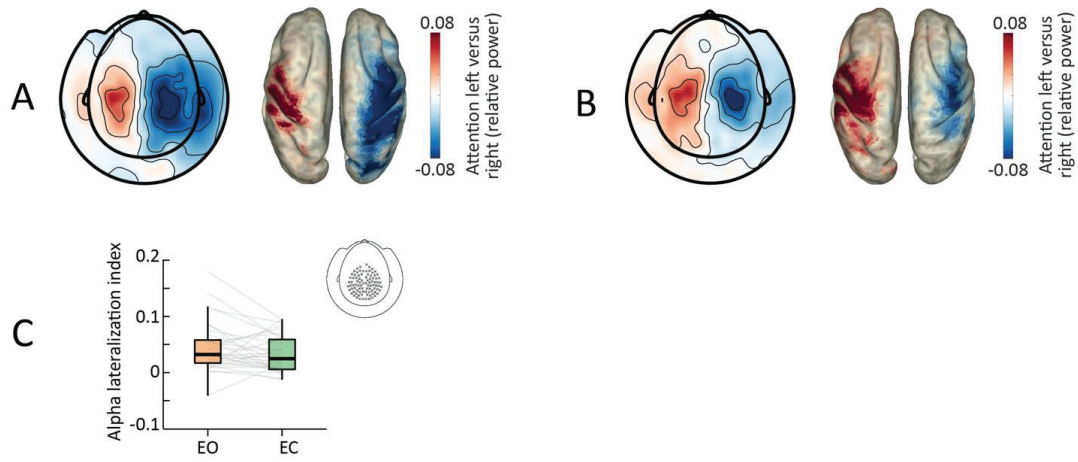
Figure 3



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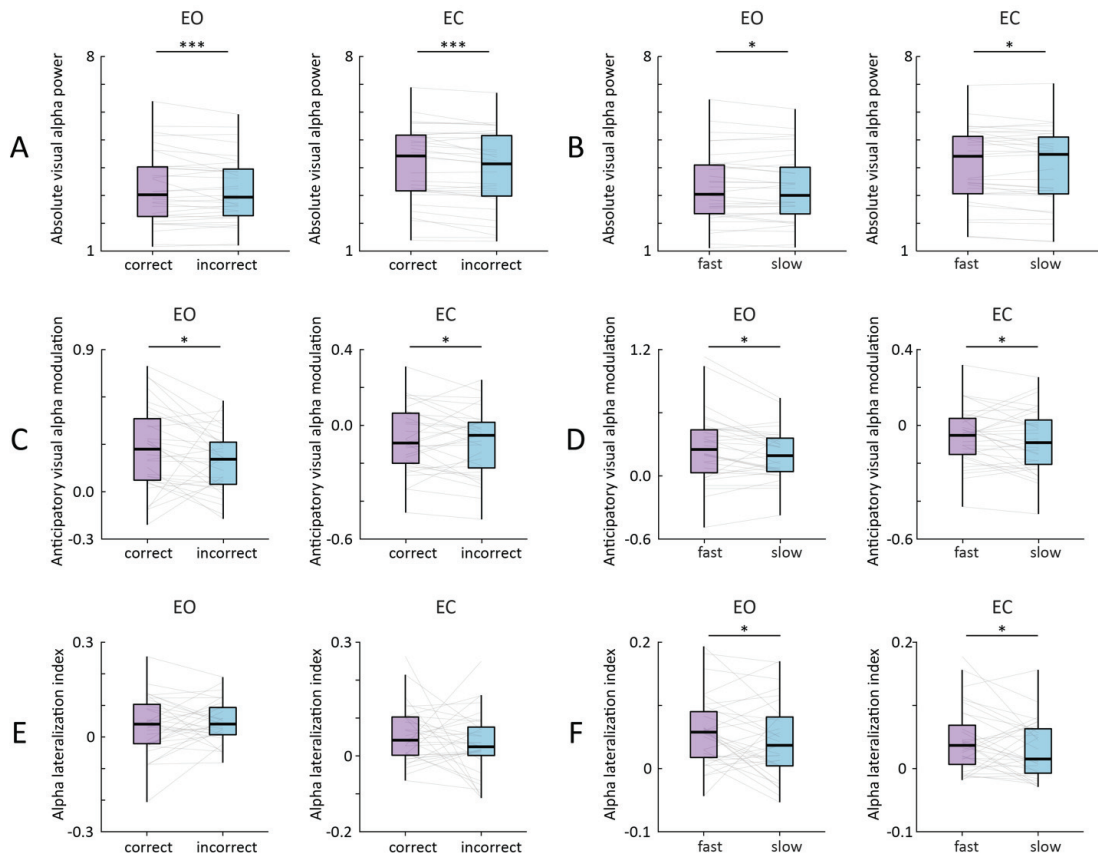
Figure 4



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Figure 5



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Figure 6

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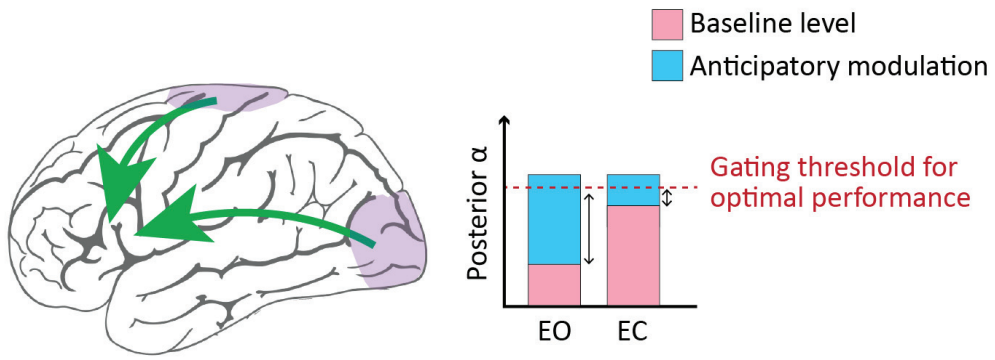
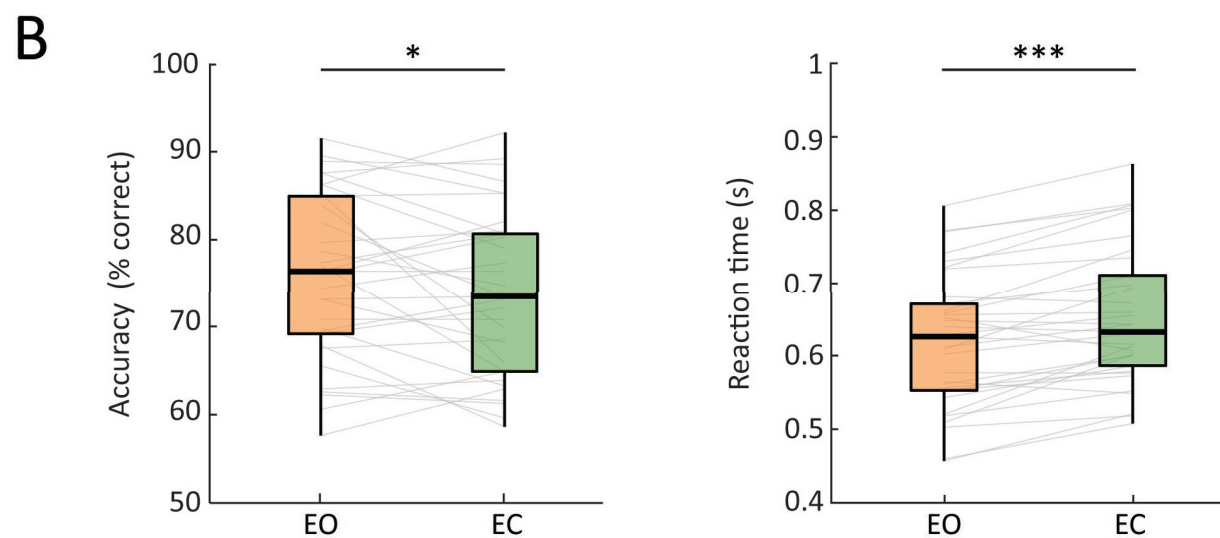
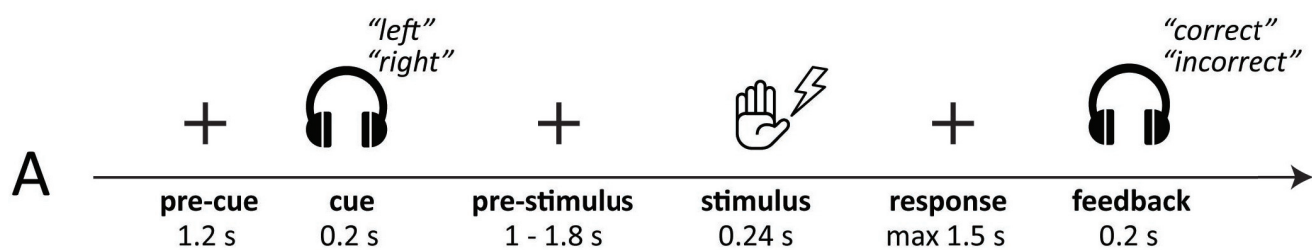
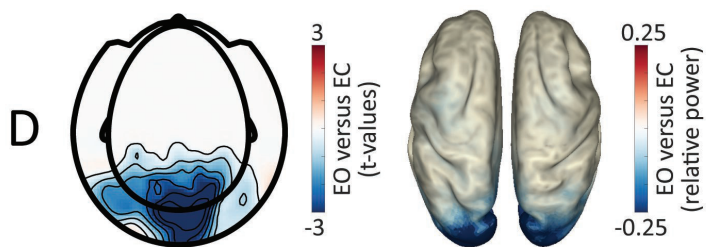
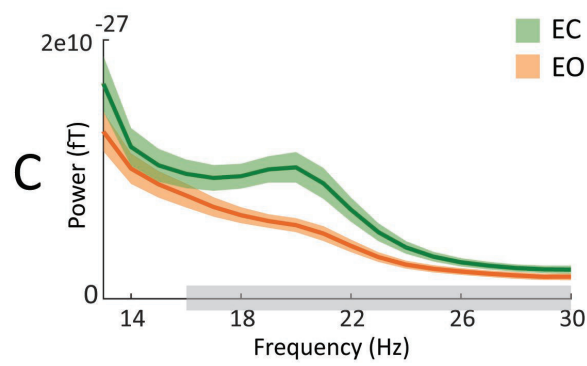
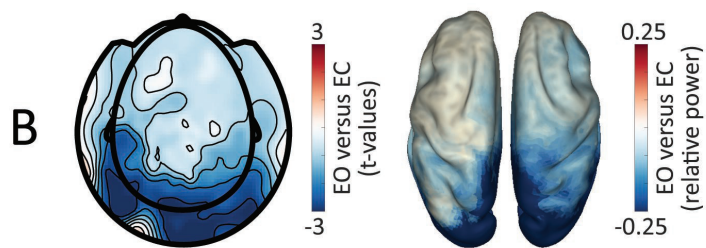
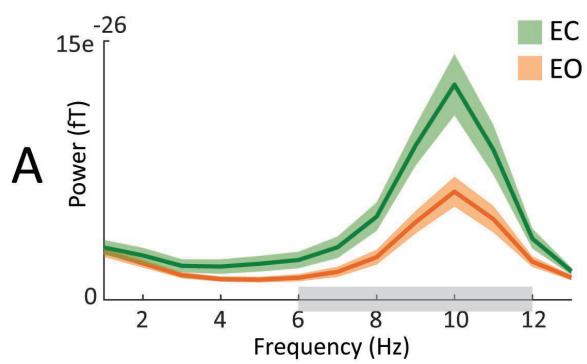
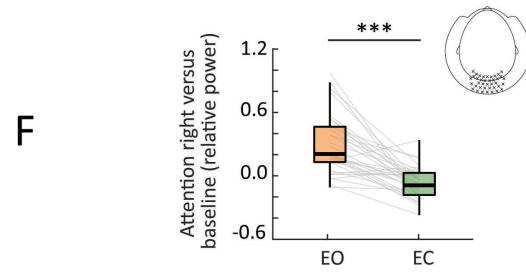
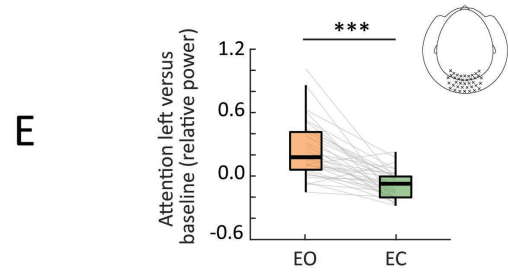
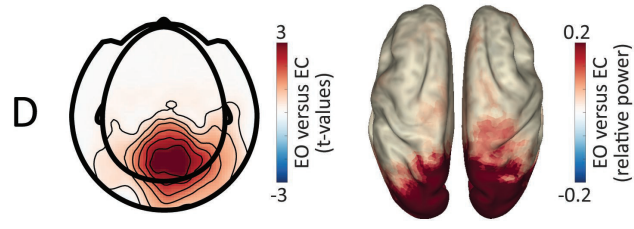
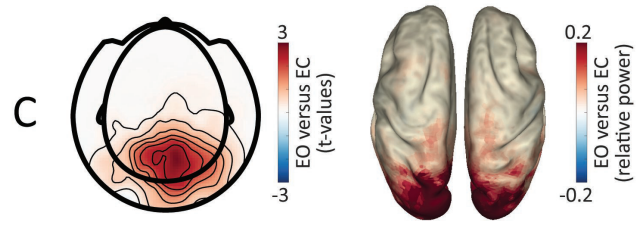
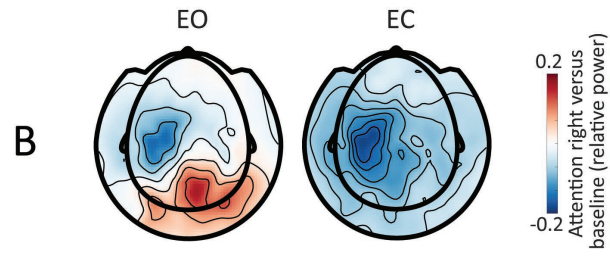
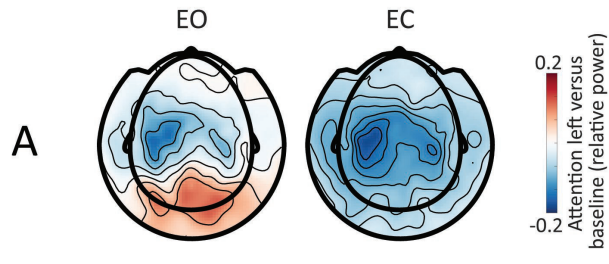


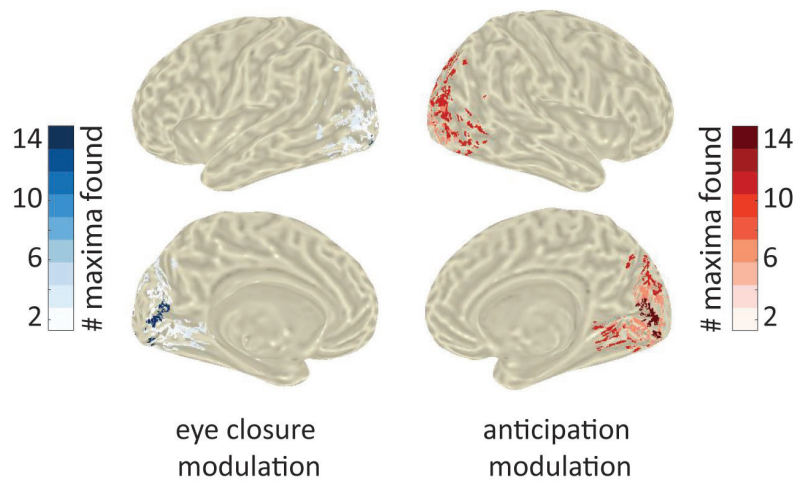
Figure 7







A



B

