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Closing eyes during auditory memory retrieval modulates alpha rhythm but does not alter tau rhythm

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17 Abstract

18 The alpha power increase that occurs when the eyes are closed is one of the most well-known effects in human
19 electrophysiology. In particular, previous psychological studies have investigated whether eye closure can boost
20 memory performance under certain circumstances, providing contradictory evidence across sensory input modalities.
21 Although alpha power is modulated during different phases of memory and these modulations are correlated with
22 performance, few studies have reported on the relationship between eye closure, memory, and alpha-band power. The
23 present study investigates the influence of eye closure while participants (n=21) performed an auditory recognition
24 memory task with spoken words during the recording of magnetoencephalography (MEG) data. Our results showed
25 no evidence for a behavioural effect of eye closure in the performance of the task. In addition, electrophysiological
26 responses to the stimuli showed the expected alpha event-related desynchronization (ERD) 0.5-1 s and a high-
27 alpha/beta event-related synchronization (ERS) 1-2 s after word onset. The data showed the expected memory effect,
28 i.e. remembered words elicited greater 10 Hz ERD than forgotten words in the brain regions typically associated with
29 the language network, suggesting a modulation of tau rhythm. Eye closure modulated alpha rhythm only in posterior-
30 parietal and occipital regions. The lack of interaction and the different localizations found for modulations of tau and
31 classical alpha rhythms suggests that these rhythms play distinct functional roles in memory performance.

32

33 Highlights:

- 34 - We studied the effect of eye-closure alpha on memory retrieval.
- 35 - We found no evidence of a behavioural effect of eye closure.
- 36 - Eye closure modulated posterior-parietal and occipital rhythms.
- 37 - Memory effects modulated the tau rhythm in language-related areas and right parietal-frontal lobes.
- 38 - **Tau and alpha rhythms seem to play distinct functional roles in auditory memory performance**

39

40 Keywords: alpha rhythm, tau rhythm, memory, eye closure, MEG

41

42 1 Introduction

43 Since alpha oscillations were first described in electroencephalographic (EEG) signals by Berger (1929) almost a
44 century ago, thousands of studies have investigated their neurophysiological origins and relationship to cognition and
45 brain function. The alpha rhythm occurs in the 7 to 13 Hz range and can be clearly detected as an increase in power
46 in posterior sensors when the eyes are closed compared to when they are open (Berger, 1929). Source reconstructions
47 have associated this power change with visual cortex (Barry et al., 2009, 2007). However, alpha is not the only rhythm
48 that fluctuates in this frequency range. Previous studies have identified two other 7-13 Hz rhythms: the mu rhythm
49 and a third rhythm (later termed tau). The mu rhythm is an oscillation present in motor-related areas, and is associated
50 with desynchronization when participants perform motor tasks (Pfurtscheller et al., 1997). Similarly, the third or tau
51 rhythm is found in the middle temporal region as a desynchronization when subjects listen to auditory stimuli and is
52 thought to be independent of posterior alpha and mu rhythms (Hari, 1993; Hari et al., 1997).

53 The aim of the present experiment was to use MEG to study how alpha-range rhythms respond to auditory
54 stimuli in an episodic memory task, with special attention to the role of eye closure. The observed pattern of alpha
55 range rhythms varies across memory tasks. Beta rhythm has been found to respond to stimuli in different memory
56 tasks along with alpha rhythm. Both alpha and beta desynchronization have been found in response to stimuli during
57 the encoding and retrieval phases of tasks involving short-term memory (e.g. Klimesch et al., 1993), semantic memory
58 (e.g. Doppelmayr et al., 2005) and episodic memory (e.g. Klimesch et al., 1997). Klimesch (1999) suggested that
59 larger decreases in alpha and beta bands reflect better cognitive and memory performance. For the encoding phase,
60 larger alpha desynchronization has been found for later remembered words compared to later forgotten words (known
61 as the subsequent-memory effect, Klimesch et al., 1997; Hanslmayr et al., 2012). For the retrieval phase, larger alpha
62 desynchronization has been found for better performers (i.e. the participants who remembered more words) compared
63 to worse performers (i.e. those who remembered fewer words, Klimesch et al., 1993). Not only has this pattern been
64 found in different memory tasks (for a review, see Klimesch, 1999; Hanslmayr et al., 2012, 2016), but also in other
65 cognitive tasks such as mental rotation (Klimesch et al., 2003; Hanslmayr et al., 2005).

66 Moreover, the magnitude of alpha desynchronization in response to a stimulus depends on the absolute power
67 of alpha in the pre-stimulus interval (Pfurtscheller and Aranibar, 1977). The larger the absolute alpha power in the
68 pre-stimulus interval, the larger the alpha desynchronization in response to the stimulus. Klimesch, Sauseng, & Gerloff
69 (2003) modulated alpha power dynamics in a mental rotation task using TMS. Higher absolute alpha power during
70 the baseline period induced greater alpha desynchronization in response to the stimuli, which resulted in better
71 behavioural performance. Similar results were reported in Hanslmayr et al. (2005) using neuro feedback training to
72 increase absolute alpha power in the baseline period.

73 **An important point for the present study is the fact that all of these studies used visual stimuli, whereas**
74 **similar modulation of memory retrieval has not been found in studies using auditory stimuli.** For instance,
75 Krause et al. used an auditory memory task with tones and found no evidence for the classical alpha event-related
76 desynchronization (ERD, Krause, Lang, Laine, Kuusisto, & Pörn, 1995). Conversely, bilateral alpha ERD was found
77 in an auditory memory task with vowels even though no modulation due to task performance was detected (Krause et
78 al., 1996). A possible explanation for these negative results using auditory stimuli may be that observing the 7-13 Hz
79 (tau) rhythm has been more elusive in EEG than in MEG or intracranial recordings (Klimesch, 1999).

80 Moreover, despite the large volume of research on alpha's role in memory and the boost in alpha in posterior
81 brain regions due to eye closure, the influence of eye closure on the role of alpha oscillations in the performance of
82 memory retrieval remains relatively understudied. The role of eye closure in memory retrieval has been examined in
83 several behavioural studies (Glenberg et al., 1998; Perfect et al., 2011, 2008; Vredeveltdt, 2011; Vredeveltdt et al.,
84 2012, 2011; Wagstaff et al., 2004). These studies report on different paradigms in which eye closure and
85 disengagement from the environment increased the number of recalled items or experiences. Glenberg et al. (1998)
86 showed that eye closure and disengagement from the environment increased the number of recalled words and were
87 able to rule out the possibility that social embarrassment produced this effect. Similarly, Wagstaff et al. (2004) found

88 enhanced memory for public events when eyes were closed at recall, and Perfect et al. (2008) showed the same effect
89 for everyday memories of both live and videotaped events. Vredeveldt (Vredevelt 2011; Vredeveldt et al., 2012, 2011)
90 reviewed several studies showing that instructing individuals to close their eyes or avert their gaze from the
91 experimenter's face significantly improved performance on a variety of cognitive tasks, particularly memory tasks.
92 Two hypotheses have been proposed to explain these performance boosts due to eye closure. On the one hand,
93 according to the cognitive load hypothesis, this memory improvement may result from freeing cognitive resources by
94 closing the eyes (Perfect et al., 2011, 2008). On the other hand, the modality-specific interference hypothesis suggests
95 that reducing visual interference by closing the eyes promotes visualization of the event and improves memory
96 (Vredeveldt, 2011; Vredeveldt et al., 2012, 2011).

97 The present study used an episodic memory task, in which the retrieval phase of the task was performed in
98 the auditory domain. This allowed participants to perform the retrieval phase with their eyes either closed or open,
99 and also allowed us to examine the existence and role of the different rhythms in the alpha range (7-13 Hz), including
100 the tau rhythm previously associated with auditory tasks. Therefore, the experiment aimed at investigating 1) how
101 rhythms in the alpha range are modulated in the retrieval phase of an episodic memory task, 2) how eye closure (visual
102 alpha modulation) interacts with these rhythms and affects task performance, and 3) whether the role of the classical
103 alpha and tau rhythms can be disentangled or are part of the same process in auditory memory tasks. We hypothesized
104 that eye closure would increase alpha power at baseline and this would elicit a larger ERD during the retrieval response
105 to a word. Based on previous behavioural results, we also hypothesized that this larger alpha ERD would help improve
106 overall performance on trials with eyes closed compared to those with eyes open.

107

108 **2 Materials and Methods**

109 The study was carried out at the Basque Center on Cognition, Brain, and Language, and was approved by its
110 institutional review board. Twenty-one native Basque-speaking, right-handed adult participants (11 male, 10 female)
111 were recruited for this experiment. All subjects were neurologically healthy, with no hearing or reading disorders. All
112 participants were screened for magnetic interference prior to data collection and provided informed consent
113 (Declaration of Helsinki) before starting the experiment. Additional data from two participants was recorded: data
114 from one participant were discarded because this participant fell asleep, and data from another were discarded because
115 s/he did not provide behavioural responses.

116

117 **2.1 Design and Materials**

118 The memory performance of participants was assessed using a recognition task containing nine blocks. Each block
119 consisted of three phases: encoding (50 trials), rehearsal (5 min) and retrieval (50 trials) for a total duration of 11
120 minutes. During the encoding phase, visual words were presented on a black back-projection screen (2 seconds per
121 word), and participants were instructed to read and memorize the list of 50 words silently. In the rehearsal phase they
122 were asked to think silently about the words they had just read. Participants were instructed that as soon as they noticed
123 they had become distracted during rehearsal, they should, start thinking about the words again. In the retrieval phase,
124 participants listened to probe words and had to recognise words that had been present in the encoding phase by pressing
125 a button with the right hand (25 trials were words to be remembered and 25 trials were words to be rejected). Subjects
126 had five seconds from the onset to reject or accept a word, **pressing a button with the right hand index finger to**
127 **accept and the middle finger to reject**. If no response was given within that time, the next word was played. If they
128 responded to a word, they had to wait the remaining time (until the full five seconds were over) to listen to the next
129 word. If more than one answer was given, only the first one was used in the analyses. Each participant performed the
130 task in two conditions. In half of the blocks, participants were instructed to perform both the rehearsal and the retrieval
131 phases of the task with eyes closed (EC); in the other half of the blocks, they were instructed to perform both phases
132 with eyes open (EO; see Figure 1). The order of the EC and EO blocks was counterbalanced across participants.
133 Participants performed the task in Basque, and the words in each list were randomly selected from a larger set of

134 words with similar frequencies ($\log_{10}(\text{freq})$, mean=1.02; std=0.69), length (mean=7; std=2.06) and syllable number
135 (mean=4; std=0.95). All the words were nouns that referred to concrete and imageable concepts in daily life.

136 After performing the task, two resting state blocks each of two-minutes duration were recorded: one block
137 with eyes closed and the other with eyes open.

138

139 **2.2 MEG data acquisition**

140 Data were recorded using a 306-channel Elekta Neuromag (Elekta Oy, Helsinki, Finland) located at the MEG
141 laboratory of the Basque Center on Cognition Brain and Language. The MEG is located in a magnetically shielded
142 room (passive shielding; Vacuumschmelz GmbH, Hanau, Germany). Participants were told to relax and find a
143 comfortable position between blocks in order to prevent movements during data acquisition; they were also instructed
144 to avoid head, body and eye movements during the task. Two (vertical and horizontal) EOG channels and a single
145 bipolar ECG lead were recorded for heartbeat and eyeblink removal by means of Independent Component Analysis
146 (ICA). A Polhemus Isotrak (Polhemus, Colchester, VM, USA) was used to record points on the head for alignment of
147 the head coordinates to each subjects structural MRI (MPRAGE, 1 mm³ voxel size). Additionally, four head
148 localisation coils were attached to the participant's head, and their spatial location (relative to fiducials) was recorded.
149 The four coils were active during the recordings to provide continuous head position information (cHPI). MEG data
150 were acquired at a 1000 Hz sampling rate, high-pass filtered at 0.03 Hz and low-pass filtered at 330 Hz during
151 acquisition.

152

153 **2.3 MEG data analysis**

154 The purpose of the first block was habituation to the task and the MEG, and these data were discarded from further
155 analysis. Only the remaining eight blocks were used for data analysis.

156

157 **2.3.1 Behavioural Analysis**

158 The proportion of trials with successful recall was modelled with a generalised linear mixed effects regression model
159 (Dixon, 2008) with the Laplace approximation as well as posterior simulation, using eye closure as a factor (i.e. open
160 and closed). Two models were compared: the first model included a participant random effect for the intercept
161 ($m_1 = \text{Hit} \sim \text{Eyes} + (1|\text{Sbj})$), whereas the second model included a participant random effect for the eye closure factor
162 ($m_2 = \text{Hit} \sim \text{Eyes} + (1 + \text{Eyes}|\text{Sbj})$).

163 A region of practical equivalence (ROPE, Kruschke, 2011) of one-item difference in memory recall was
164 defined to establish if there were behavioural differences between the eyes-closed and eyes-open conditions. In other
165 words, eye closure would be considered to have an effect on behaviour only if performance in the two conditions (eyes
166 closed and eyes open) differed by at least one item.

167

168 **2.3.2 MEG data preprocessing**

169 Using MaxFilter 2.2, the recorded MEG data were filtered using temporal Source Space Separation (tSSS) (Taulu and
170 Simola., 2006) with a four-second time window and a minimum correlation of 0.98. Head origins and bad channels
171 were supplied manually for each participant. Data were downsampled to 250 Hz, and line frequency (50 Hz) and
172 harmonics were filtered. Following recommendations from the MEG laboratory at the MRC Cognition and Brain
173 Sciences Unit (http://imaging.mrc-cbu.cam.ac.uk/meg/Maxfilter_V2.2), the downsampling and filtering were
174 conducted in two separate steps.

175 Next, data were preprocessed using the Fieldtrip toolbox (version 20141202, (Oostenveld et al., 2011)). First,
176 data from the retrieval period were segmented into epochs. The epochs were time locked to the onset of the word.

177 Data were segmented into five-second epochs consisting of two seconds before the onset of the trial and three seconds
178 following the onset of the trial. The data were then screened for jump and other noise artefacts, padded to 12 seconds
179 per trial and then filtered with a low-pass FIR filter at 40 Hz (one pass-zero phase), and the resulting epochs were
180 normalized relative to the baseline period and detrended with respect to the whole interval. For further eye and
181 heartbeat artefact reduction, data were decomposed using the fastICA algorithm with the number of components set
182 equal to the number of sensors (204 gradiometers). No data dimension reduction algorithm was applied prior to ICA.
183 Then, the correlation of each ICA component time course with the HEOG, VEOG, and ECG time courses was
184 calculated. Components whose correlation exceeded three standard deviations from the mean correlation in any of
185 these cases (HEOG, VEOG, or ECG) were removed before back projecting the single-trial data into the original sensor
186 space.

187

188 **2.3.3 MEG data analysis of eye-closure effect**

189 First, alpha power modulations due to eye closure both during the resting state and retrieval phases were compared.
190 For this analysis, the first 30 seconds of the resting state with eyes closed, and with eyes opened were used. In addition,
191 the first 30 seconds of the retrieval phase of the first blocks with eyes closed and with eyes opened were extracted for
192 each participant. Power values were calculated using a single Hanning taper based on frequency dependent window
193 length. There were six cycles per time window, which was sliced in steps of 1 s. The analysis was performed on the
194 whole epoch (30 s) between 0 and 40 Hz in steps of 1 Hz. This resulted in linearly variant frequency smoothing of 1.7
195 Hz at 10 Hz. Absolute power values were used for this analysis. Then, gradiometers were combined, and the statistical
196 analyses were performed on the combined gradiometers.

197 A statistical analysis of alpha power was conducted to test the eye-closure effect. A randomisation
198 distribution of cluster statistics (Maris and Oostenveld, 2007) was constructed over sensors, with power averaged
199 across frequency and time, and used to evaluate whether there were statistically significant differences between
200 conditions in the alpha band (7-13 Hz). In particular, t-statistics were computed for each sensor and a clustering
201 algorithm formed groups of channels over time points based on these tests. The neighbourhood definition was based
202 on the template for combined gradiometers of the Neuromag-306 provided by the Fieldtrip toolbox. The threshold for
203 a data point to be included in a cluster was set at $p=0.05$ (based on a two-sided dependent t-test, using probability
204 correction), with at least two neighbours. The sum of the t-statistics in a sensor group was then used as a cluster-level
205 statistic (i.e., the maxsum option in Fieldtrip, named clusterstat in the Results section), which was then tested using a
206 randomisation test with 1000 runs.

207

208 **2.3.4 MEG time-frequency analysis of retrieval phase**

209 The oscillatory power of the retrieval phase was examined calculating Event Related Synchronizations (ERS) and
210 Desynchronizations (ERD). A single Hanning taper based on frequency dependent window length (six cycles per time
211 window) that was sliced in steps of 0.05 s was used. The analysis was performed on the whole trial (between -2 and 3
212 s) and between 0 and 40 Hz in steps of 1 Hz. This resulted in linearly variant frequency smoothing of 1.7 Hz at 10 Hz.
213 Power values for each time-frequency point were normalised relative to the baseline period (-0.5, 0) s. Afterwards,
214 gradiometers were combined, and statistical analyses were performed on the combined gradiometers in two ways:

215 **A restricted statistical analysis** was performed to test the hypothesis outlined in the introduction: alpha ERD in the
216 retrieval phase is larger for remembered than forgotten items. Moreover, eye closure should elicit larger alpha ERD
217 compared to the eyes-open condition. For the statistical analysis, a randomisation distribution of cluster statistics
218 (Maris and Oostenveld, 2007) was performed in the alpha band (7 - 13 Hz) during the (-0.5, 2) s time window. The
219 rest of the parameters remained the same as in the previous statistical analyses.

220

221 **An unrestricted frequency** analysis was performed to complement the previous analysis and check for any effects
222 in other frequency bands that had not been considered in the hypothesis. Thus, a randomisation distribution of

223 cluster statistics was performed on all the frequencies during the (-0.5, 2) s time window. The rest of the parameters
224 remained the same as in the previous statistical analyses.

225

226 **2.3.5 MEG source level analysis**

227 Dynamic Imaging of Coherent Sources (DICS) (Gross et al., 2001) was used for source reconstruction. Structural MRI
228 were segmented into scalp, skull, brain and CSF, and a volume conduction model was constructed based on this
229 segmentation using a single shell approximation (Nolte, 2003) by assigning conductivity to the brain. An 8 mm grid
230 (available in Fieldtrip) was used to construct the leadfields. Cross-spectral density matrices were calculated around 10
231 Hz (with a smoothing window of 3 Hz) for three time windows of interest: (0.5, 1.0), (1.0, 1.5) and (1.5, 2) s. For each
232 time window of interest, complex spatial filters (common to the four conditions) were constructed using the leadfields
233 and the cross-spectral density matrices of the window and the baseline (-0.5, 0) s. Afterwards, data were filtered using
234 the common filters and the power changes relative to baseline were calculated for each condition.

235 For the statistical analysis, a randomisation distribution of cluster statistics (Maris and Oostenveld, 2007)
236 was performed in each of the time windows (0.5, 1.0), (1.0, 1.5) and (1.5, 2) s. The rest of the parameters remained
237 the same as in previous statistical analyses.

238

239 **2.3.6 Power Spectrum analysis of the retrieval phase**

240 **As a post-hoc analysis, the power spectrum of the retrieval phase of each trial (between -2 and 3 s) was**
241 **computed using a single Hanning taper for a frequency range between 1 and 40 Hz. Afterwards, gradiometers**
242 **were combined, and mean power spectrum was calculated for posterior occipital channels and right temporal**
243 **channels separately. The peak frequency in the 7 – 13 Hz frequency band was calculated per subject for each**
244 **condition and the grand average for each of the channel groups.**

245 For the statistical analysis, a paired t-test comparing peak frequencies in occipital and right temporal
246 channels was performed for each of the conditions and for the grand average.

247

248 **3 Results**

249 **3.1 Behavioural Analysis**

250 The performance of the participants was on average around 0.75 for both models and did not differ across conditions.
251 When the two models were compared, no benefit of including the participant random effect of eye closure
252 ($\Pr(>Chisq)=0.96$) was found. Therefore, only the first model with a participant random effect for the intercept is
253 reported ($m1=Hit \sim Eyes + (1+1|Sbj)$). Based on this model, participants' proportion (95% CI) of correct trials was
254 0.75 (0.70, 0.79) in the eyes-closed blocks and 0.76 (0.67, 0.82) in the eyes-open blocks.

255

256 **3.2 MEG data**

257 **3.2.1 Eye-closure effect**

258 Figure 2 displays the power difference in the alpha band (7 - 13 Hz) between eyes closed and eyes open for both the
259 resting state (a) and retrieval phases (b). Although both images indicate an alpha increase in posterior sensors and
260 have very similar topographies, the alpha power difference in the retrieval phase is smaller (see colour bars). The
261 statistical analysis for each EC-EO comparison revealed a positive cluster for the resting state comparison
262 (clusterstat=343.5; $p<0.001$) and another positive cluster near the significance threshold for the retrieval phase
263 (clusterstat=11.91; $p=0.073$).

264

265 3.2.2 Time-frequency analysis

266 Restricted statistical analysis

267 Figure 3 illustrates the time-frequency response to the spoken word stimulus and Figure 4 illustrates a summary of the
268 results of the oscillatory power analysis both at the sensor and source levels. The grand average (see Figure 3A and
269 Supplementary material, Figures S1-S4) shows the expected response to a spoken word stimulus: theta ERS between
270 0 and 0.5 s, and alpha ERD between 0.5 and 1 s, followed by a high-alpha/beta rebound between 1 and 2 s. This was
271 found for all conditions (eyes closed and eyes open) and items (remembered and forgotten, see Figure 3B). The alpha
272 ERD between 0.5 and 1 s was mainly found in left temporal and posterior occipital sensors (see Figure 3A). The
273 differences described below are a modulation of this pattern, revealing an ERD effect related to type of item
274 (remembered vs. forgotten) but an ERS effect for eye closure (eyes closed vs. eyes open).

275 Comparing the different conditions, the data are consistent with the expected memory effect insofar as the
276 remembered items were associated with greater alpha ERD compared to forgotten items, in both the eyes-closed and
277 eyes-open conditions. For the eyes-closed condition, the a priori statistical analysis in the alpha band (7-13 Hz)
278 revealed a cluster (clusterstat=-2214; $p=0.002$) that lasted between 0.6 and 1.75 s (Figure 4A, bottom row). For the
279 eyes-open condition, a significant cluster (clusterstat=-1470; $p=0.006$) was found between 0.65 and 1.65 s (see Figure
280 4A, top row).

281 Moreover, an eye-closure effect was also found. For both types of items (remembered and forgotten) there
282 was stronger alpha ERS between 1 and 2 s in the eyes-closed compared to the eyes-open condition. For the
283 remembered items, a significant cluster was found between 1 and 2 s (clusterstat=1401; $p=0.02$) (see Figure 4B, top
284 row). For the forgotten items, there was also a significant cluster (clusterstat=1714; $p=0.002$) between 1 and 2 s (see
285 Figure 4B, bottom row).

286 For visualization of the topographies of these patterns, the effect was split into three different half-second
287 time windows: 1) from 0.5 to 1 s (see Figure 4, first column) where the strongest alpha ERD was present for the
288 memory comparison; 2) from 1 to 1.5 s (see Figure 4, second column) where the alpha ERD was still present for the
289 memory comparison but there was also strong support for alpha ERS in the eye-closure comparison; and 3) from 1.5
290 to 2 s (see Figure 4, third column) where the alpha ERS was strongly supported in the eye-closure comparison, with
291 less strong support for the alpha ERD effect in the memory comparison.

292 The topography plots show that the memory effect in the initial period (from 0.5 to 1 s) appears as alpha ERD
293 spread across almost all the sensors, but with the main focus in temporal sensors, especially right temporal sensors
294 (see Figure 4A, first column). The effect appears to be due to either greater ERD or less ERS for later remembered
295 items, depending on the sensor location. As time evolves, the alpha ERD only remains on the temporal sensors of both
296 hemispheres (see Figure 4A, second and third columns). In contrast, the eye-closure ERS effect is mainly found at
297 posterior and parietal sensors (see Figure 4B). Although the topography is maintained across time, the magnitude of
298 the effect increases in the later time intervals.

299 Statistical analyses were performed to test interactions. One analysis tested the modulation of eyes closed
300 (Eyes closed vs Eyes open) on the item type effect (Remembered – Forgotten). The other analysis tested the
301 modulation of item type (Remembered vs Forgotten) on the eyes closed effect (Eyes closed-Eyes open). Neither
302 analysis revealed any statistically significant cluster ($abs(clusterstat)<259$; $p>0.7$).

303

304 Unrestricted statistical analysis

305 For the unrestricted frequency analysis, the analysis schema of the a priori analysis was maintained, but instead of
306 focusing only on the alpha band, all frequencies from 3 to 40 Hz were included (see Supplementary material, Figures
307 S5-S8).

308 The results were similar to those for the restricted alpha band analysis: remembered items showed greater

309 alpha ERD compared to forgotten items, for both the eyes-closed and eyes-open conditions. For the eyes-closed
310 condition, the statistical analysis revealed one significant cluster (clusterstat=-8281; $p=0.002$) in a 4 - 27 Hz band,
311 during the 0.65 - 1.8 s time window (see Figure 4A, bottom row time-frequency plot, and Supplementary material,
312 Figure S5). For the eyes-open condition, the analysis revealed one significant cluster (clusterstat=-7357; $p=0.004$) in
313 a 4 - 22 Hz band during a 0 - 2 s time window (see Figure 4A, top row time-frequency plot, and Supplementary
314 material, Figure S5). Note that although the cluster spans a large time window, this is only true for the low frequencies
315 around theta. For the rest of the frequencies, the time window approximately overlaps the time window of the eye-
316 closure effect.

317 An eye-closure effect similar to that in the a priori analysis was also found, but it included a wider range of
318 frequencies. For both types of items (remembered and forgotten), the eyes-closed condition elicited stronger alpha
319 ERS between 0.6 and 2 s than the eyes-open condition but, in addition, the effect included beta ERS. For the
320 remembered items, the statistical analysis supported a significant cluster (clusterstat=14766; $p=0.01$) between 8 - 38
321 Hz over the interval of 0.6 - 2 s (see Figure 4B, top row time-frequency plot, and Supplementary material, Figure S5).
322 For the forgotten items, there was a cluster (clusterstat=13840; $p=0.006$) between 7 - 27 Hz, over the interval of 0.8 -
323 2 s (see Figure 4B, bottom row time-frequency plot, and Supplementary material, Figure S5). This analysis revealed
324 that, in addition to the alpha band, the beta band during the retrieval phase was also modulated by eye closure.
325 Moreover, the time windows for the memory and eye-closure effects seemed to overlap more than in the restricted
326 analysis.

327 In the early phase, the memory effect was mainly found in the alpha band as greater ERD or reduced ERS
328 for remembered items compared to forgotten items, in both the eyes-closed and eyes-open conditions. Compared to
329 the restricted analysis, it included part of the beta band. Similar to the restricted analysis, the largest magnitude for the
330 effect was found in right temporal sensors. On the other hand, an equivalent eye-closure effect was found in alpha and
331 beta bands, as a greater ERS for eyes closed compared to eyes open. The effect was mainly found in posterior and
332 right-parietal sensors.

333 Statistical analyses were performed to test for interactions (the same as for the a priori analysis). Similar to
334 the restricted analysis, the results did not reveal any significant clusters ($\text{abs}(\text{clusterstat}) < 259$; $p > 0.71$).

335

336 3.2.3 Source level analysis

337 Figure 4 also illustrates the results of the power analysis at the source level for each of the time windows, depicted
338 below the corresponding topography. The grand averages for the three time windows show overall brain
339 desynchronization in the alpha rhythm (7-13 Hz) (see also Supplementary material, Figures S9-S11).

340 Comparing different conditions, the data are partially consistent with the sensor level analysis. In the first
341 time window (0.5 - 1.0 s) (see Figure 4, first column), the statistical analysis only showed differences between
342 forgotten and remembered words for the eyes-open condition. The cluster was localized in the right posterior inferior
343 temporal and right occipital lobes (clusterstat=-684.17; $p=0.035$).

344 In the second time window (1.0, 1.5 s), the statistical analysis captured both item and eye-closure effects (see
345 Figure 4, second column). For the eyes-open condition, remembered words showed greater alpha ERD in the left IFG,
346 posterior STG and angular gyrus (clusterstat=-889.23; $p=0.017$). For the eyes-closed condition, remembered words
347 showed greater alpha ERD in the right parietal and frontal lobes (clusterstat=-1155.2; $p=0.008$). For remembered
348 words, the eyes-closed showed less alpha ERD than the eyes-open condition in the occipital and posterior-parietal
349 lobes (clusterstat=645.15; $p=0.049$).

350 In the third time window (1.5, 2 s), the statistical analysis showed only an eye-closure effect (see Figure 4,
351 third column). Both remembered and forgotten words with eyes closed showed less alpha ERD than in the eyes-open
352 condition, revealing two significant clusters in the occipital and posterior-parietal areas (clusterstat=2931.1; $p=0.001$
353 and clusterstat=1184.5; $p=0.005$).

354 Statistical analyses were performed to test for interactions (the same as in the previous two analyses). The
355 results did not reveal any significant clusters ($\text{abs}(\text{clusterstat}) < 222.94$; $p > 0.18$).

356

357 **3.2.4 Power Spectrum analysis of the retrieval phase**

358

359 **Figure 5 shows the mean Power Spectrums of the different channel groups (occipital and right temporal) in all**
360 **the conditions. Table 1 summarizes the results of the statistical analyses of the peaks in the power spectrum,**
361 **showing the mean peak frequency and standard deviation (in Hz) for each condition and channel group. The**
362 **statistical analysis did not reveal any differences between the peak frequencies of right temporal and occipital**
363 **channels in any of the conditions.**

364

Table 1 around here

365 **4 Discussion**

366 **Summary of main findings**

367 In this experiment, participants recognized spoken words in a recognition memory task conducted in MEG either with
368 their eyes open or their eyes closed. Oscillatory power analysis of the MEG signals recorded in the task showed that
369 successful memory was associated with greater alpha-band desynchronization (ERD) in the half-second interval after
370 word presentation. Moreover, the oscillatory analysis showed two types of modulations in neuronal oscillations due
371 to eye closure. The first was the traditional posterior alpha power increase related to eye closure, which occurs during
372 the resting state and also, with smaller amplitude, during the retrieval phase (see Figure 2). The second modulation
373 due to eye closure was a modulation of power in alpha and beta bands in response to the stimuli. In both bands, the
374 ERS effect was greater in the eyes-closed compared to the eyes-open condition at occipital and right parieto-temporal
375 sensors. The alpha band eye-closure effect was source localised in the occipital and posterior-parietal areas, for both
376 remembered and forgotten items. While posterior alpha modulation due to eye-closure might be expected based on
377 the frequently observed association between eye closure and higher absolute posterior alpha power, modulation of
378 beta power due to eye closure has not been reported to date in the literature.

379 No evidence of a behavioural effect due to eye closure was found. Similarly, for both alpha-ERD and high-
380 alpha/beta-ERS, no statistical support for an interaction between eye closure and item type effects was found.
381 Nevertheless, modulations of alpha-ERD due to item type (remembered vs. forgotten) were found in both the restricted
382 and unrestricted analyses at similar frequency bands, time windows and sensor locations. On the other hand, the
383 unrestricted analysis revealed an effect of eye closure with ERS modulations in both the alpha and beta frequency
384 bands.

385

386 **Event-related responses during memory retrieval**

387 Previous studies have shown that during the retrieval phase of a memory task where the presented stimulus is to be
388 categorized as new or old, alpha desynchronization occurs in response to the stimuli (Klimesch, 1999; Klimesch et
389 al., 2003; Schack and Klimesch, 2002). Moreover, better performance has been linked to greater alpha ERD
390 (Doppelmayr et al., 2005; Hanslmayr et al., 2005; Klimesch, 1999; Klimesch et al., 1997). Data from this experiment
391 also demonstrated the expected memory effect: the power decrease in the alpha frequency range was larger for
392 remembered than for forgotten items. Previous EEG studies reported an alpha modulation in electrodes consistent
393 with posterior sources, while the effects found in this study also included MEG temporal (planar gradiometer) sensors.
394 The source level analysis located the effect in the left superior temporal and IFG areas for the eyes-open condition.
395 For the eyes-closed condition the effect was found in the right parietal and frontal lobes. Differences in the overall
396 sensitivity of EEG and MEG might explain the different localization of results in the present experiment compared to
397 results from previous studies. Alternatively, while the previously mentioned studies used visual stimuli, this study

398 presented auditory stimuli to the participants in order to be able to study the potential effects of eye closure on retrieval.
399 Note that Krause et al. (1996) also tested auditory memory and, even though they found bilateral alpha ERD in
400 response to stimuli in the retrieval phase, alpha ERD was not modulated by performance.

401

402 **Tau and alpha rhythms measured by EEG and MEG**

403 As Klimesch (1999) suggests, the reason that the modulation of the classical alpha rhythm often seen in the visual
404 domain is not found for the auditory domain might be because auditory stimuli instead modulate the tau rhythm in the
405 temporal lobe. Lehtelä et al. (1997) showed that in addition to the 10 Hz parieto-occipital alpha and 10 Hz rolandic
406 mu rhythms, there is a 10 Hz spontaneous oscillation that originates in the temporal lobe (also referred to as tau
407 rhythm). They found that this 10 Hz tau rhythm was suppressed, especially in the right temporal area, in response to
408 auditory stimuli, for a period starting immediately after the stimulus and lasting for about 1.5 s. Earlier, Niedermeyer
409 (1990) reported the existence of rhythmical activity over the temporal lobes, clearly separable from the posterior alpha
410 captured by epidural recordings but almost undetectable by scalp EEG electrodes. Moreover, this rhythm did not
411 respond to motor activity. Later, after studying epidural recordings of a 20-year-old female in different experimental
412 conditions such as resting, sleeping or singing, Niedermeyer (1991) named this rhythm the third or tau rhythm. The
413 tau rhythm was most readily observed in the waking state but also persisted into drowsiness and even light sleep.
414 During rest the tau rhythm was most pronounced in the posterior and anterior temporal lobe. As for sleep recordings,
415 NREM sleep stage spindles were localized in the same left posterior epidural lead while the tau rhythm was localized
416 in bilateral anterior temporal lobes. No modulation of tau rhythm was found in response to loud bang stimuli. However,
417 the tau rhythm was desynchronized while singing a song. Based on these observations, Niedermeyer concluded that
418 this temporal alphoid (10 Hz) rhythm was independent of the other two alphoid rhythms: posterior alpha and rolandic
419 mu rhythms (Niedermeyer, 1991).

420 The tau rhythm is almost undetectable using EEG (Niedermeyer, 1997). Nonetheless, tau rhythm is detectable
421 in epidural recordings (Niedermeyer, 1991, 1990) and also using MEG (Lehtelä et al., 1997). The experiment
422 presented here used auditory stimuli in the retrieval phase and recorded neural data using MEG. In fact, the results
423 showed performance-related modulation of a 10 Hz rhythm in temporal and parietal areas, an effect not yet found in
424 the EEG literature (Klimesch, 1999; Krause et al., 1996). Bastiaansen et al. (2001) also observed different alpha ERD
425 modulation patterns depending on recording modality. They found that preceding visual knowledge of results, ERD
426 in the alpha range was maximal in occipital areas in both EEG and MEG recordings. However, with auditory
427 knowledge of results, ERD in the alpha range was maximal in temporal cortex for two out of 5 participants only in
428 MEG recordings, with no ERD found in EEG recordings. A recent study carried out using MEG showed that
429 successful long term memory encoding was reflected in a power decrease in the alpha range in the sensory region of
430 the to-be-attended modality (Jiang et al., 2015). The modulations were predictive of individual memory performance.
431 Moreover, they found power increases in the alpha range in the sensory regions of the to-be-ignored modality and
432 suggested that these increases might serve to suppress this modality.

433 Consequently, in agreement with Klimesch (1999), we suggest that memory experiments using auditory
434 stimuli modulate the tau rather than the classical alpha rhythm, and therefore, MEG and/or intracranial recordings are
435 more appropriate recording methods than scalp EEG measurements. This further suggests that the functional role of a
436 given modulation (e.g., ERS or ERD) of a rhythm depends not only on its frequency range and time interval, but also
437 on the specific brain network that is responsible for generating the rhythm. The role of a 10-Hz modulation of a
438 posterior, visual cortex rhythm may not be the same as, for example, the modulation of a 10-Hz temporal, auditory
439 cortex rhythm, even if the physiological implementation of the modulation is similar in the two cases.

440

441

442 **Eye closure and event-related oscillations modulation**

443 The eye-closure effect observed in the ERS in the beta band might be interpreted as an extension of the modulation
444 seen in the range of the alpha band due to a broadening of the spectral peak when alpha-band power increases to
445 include the neighbouring bands (theta and beta). Barry et al. (2007) reported a similar modulation in beta band when
446 they studied the effect of eye closure on different frequency bands during the resting state with higher beta-band power
447 for eyes closed in posterior and right parietal EEG electrodes. On the other hand, beta-ERS could also be explained
448 as post-movement beta rebound (Pfurtscheller et al., 1998, 1996). After motor activity, power in the beta band of
449 motor cortex shows ERS. In this scenario, modulation of beta-ERS would be linked to somatosensory or motor
450 differences between conditions. A beta rebound can be modulated by different factors, for example, the force of a
451 movement (Fry et al., 2016) or the correctness of an observed action (Koelewijn et al., 2008). To the best of our
452 knowledge, no study has compared the beta-rebound with and without eyes-closed. However, it is plausible that
453 making a finger movement to press a button has a different effect when the eyes are open (providing visual feedback
454 for the movement) than when the eyes are closed (there is no visual feedback). This difference could explain the beta-
455 band modulation seen in this experiment, although the beta-ERS modulation was mainly found in posterior sensors
456 and not in sensors close to the motor cortices. Since the topography of the beta increase was more similar to the classic
457 alpha eye-closure effect, as well as to the topography reported in Barry et al. (2007), we suggest that the beta-ERS
458 modulation due to eye closure observed in this particular study was more likely to be an extension of the alpha-band
459 eye-closure effect.

460 As a methodological aside, it should be noted that the comparison between eyes open and closed conditions
461 might involve a difference in baseline power, in addition to any post-stimulus change in power. However, the greater
462 beta-ERS seen in the eyes-closed condition is a larger relative change from a baseline that already has larger spectral
463 power (see Figure 2). This indicates that power differences in the eyes closed ERS are larger in absolute terms than in
464 the eyes-open condition.

465

466 **Link between alpha and tau rhythms due to eye closure effects**

467 Perhaps the most striking feature of the current data is that the dynamics of the alpha/tau-band in the power responses
468 do not show greater ERD for the response due to eye-closure, but rather a later ERS for both alpha and beta. Although
469 our initial expectation was a classical alpha modulation due to eye closure, it is important to note that the response to
470 an auditory word is activity related to perception and word comprehension. In contrast to the differences shown in
471 absolute power during the resting state, our results indicate that the dynamics in different bands in response to a word,
472 and here, to eye closure seem to relate to late ERS. Furthermore, eye closure was not associated with either a benefit
473 or an impairment in behavioural performance. This reinforces our intuition that tau is the rhythm modulated by the
474 memory effect in this paradigm while posterior alpha-beta is modulated by eye closure, with no direct interaction
475 between these two modulations. Furthermore, no statistical support for a difference in the frequency peaks between
476 the conditions in the 7 – 13 Hz band was found (see Figure 5). These results are consistent with those found by
477 Niedermeyer (1991) where the spontaneous third (i.e. tau) rhythm was not modulated by eye closure. On the other
478 hand, the source level analysis of the data showed that eye closure modulated the localisation of the remembered vs.
479 forgotten effect: the effect was found in the language network with eyes open, whereas it was found in the right parietal
480 and frontal lobes with eyes closed (see Figure 4 and Supplementary Material, Figures S9-S11). However, no difference
481 was found when interactions were tested statistically.

482 Finally, the results of the present experiment are consistent with the modality-specific interference theory,
483 which suggests that reducing visual interference by closing the eyes promotes visualization of the event and potentially
484 improves memory of visual stimuli, but would not help memory in other modalities (Vredeveldt et al., 2012, 2011).
485 In this case, participants had to encode linguistic material. Recalling this material in the retrieval phase relies on the
486 language network encompassing bilateral speech perception areas and left perisylvian language areas. Based on the
487 oscillatory analysis results, it appears that modulating posterior alpha by closing the eyes does not directly affect
488 processing efficiency in the language network, and as a result there was no improvement or detriment in memory
489 performance due to eye closure in this task.

490

491 **5 Conclusions**

492 In this auditory word recognition experiment the expected memory effect was found: greater ERD in the alpha
493 frequency range for remembered words compared to forgotten words. This effect was mainly found in temporal
494 sensors rather than in posterior sensors. The source level analysis localized the effect in the language network and in
495 the right parietal and frontal lobes. This is evidence that auditory or spoken linguistic stimuli modulate the tau rhythm
496 while eye closure modulates posterior alpha. **The lack of interaction between these two modulations in our
497 experiment suggests that tau and posterior-alpha should be considered as two rhythms with distinct functional
498 roles in memory performance.** This would explain why eye closure did not enhance the memory performance of
499 participants in this particular environment, also supporting the modality-specific interference theory for the effect of
500 eye-closure on behavioural performance.

501

502 **6 Acknowledgements**

503 We would like to thank Dr. Doug J. Davidson for all his help in this study, and Magda Altman for her help in editing
504 the manuscript. This research was possible thanks to the support of the “Severo Ochoa Program for Centres/Units of
505 Excellence in R&D” (SEV-2015-490). AB was supported by the Basque Government (Eusko Jaurlaritza) under the
506 program “Ikertzaile ez doktoeren doktoretza-aurreko formakuntza programa” (grant reference PRE 2015_2_0208),
507 CCG was supported by the Spanish Ministry of Economy and Competitiveness through the Juan de la Cierva (IJCI-
508 2014-20821) and Ramon y Cajal (RYC-2017-21845) Fellowships.

509

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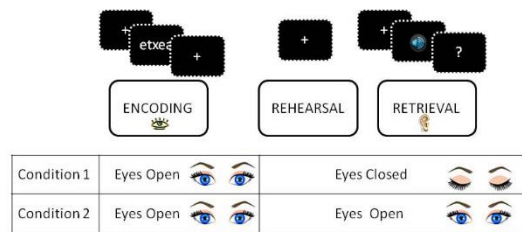
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603

604 Figures



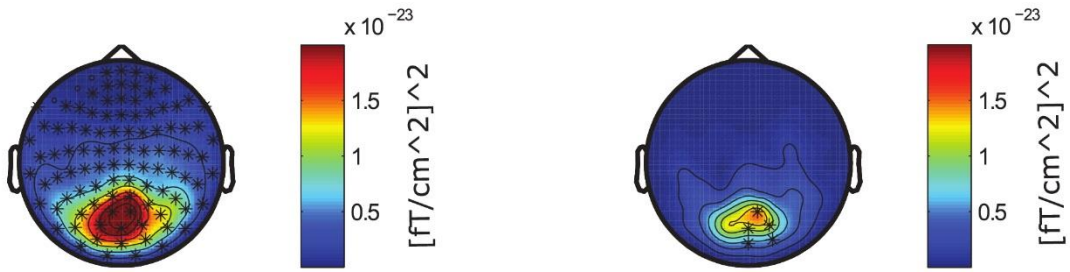
605

606 Figure 1. Design of the experiment. The first (encoding) phase of the experiment was done with the eyes open, using
607 visual stimuli. The second (rehearsal) and third (retrieval) phases were performed in two conditions: Eyes closed and
608 eyes open, with auditory stimuli.

609

a) Resting State

b) Retrieval Phase

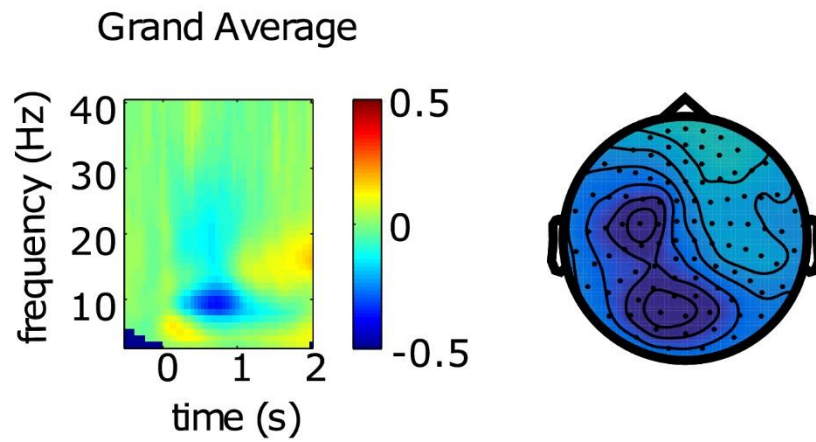


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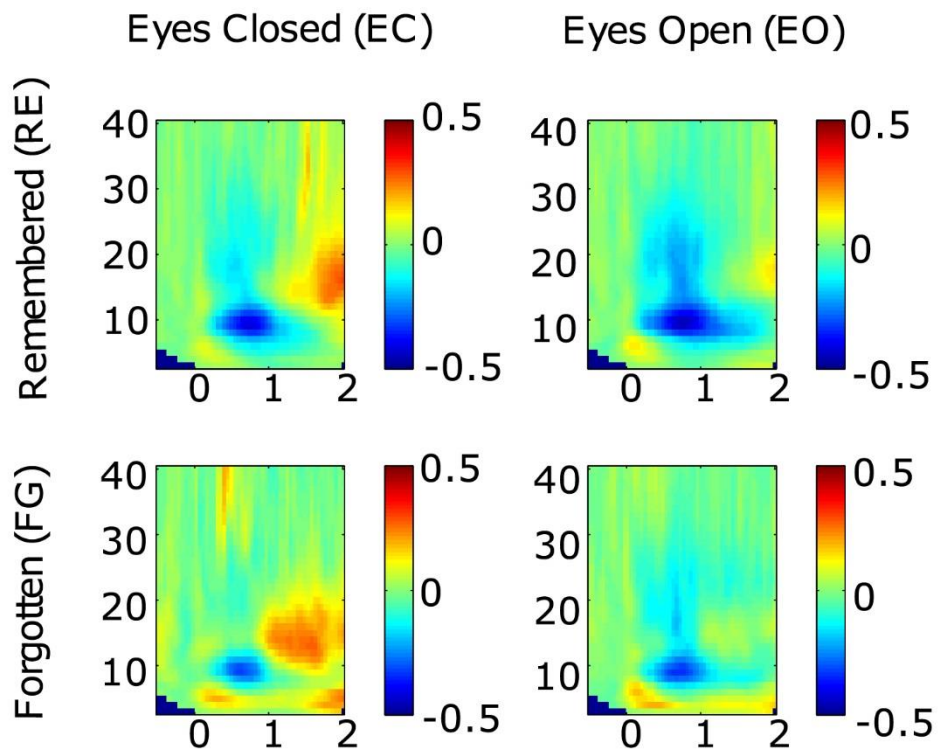
611 Figure 2. Alpha band power analysis. Alpha band (7 - 13 Hz) absolute power difference topographic distribution
612 between eyes closed and eyes open, for the resting state (A) and retrieval (B) phases. Warmer colours denote greater
613 power for eyes closed, and cooler colours denote small or almost no differences. Asterisks mark the sensors that were
614 part of the cluster resulting from the statistical analysis.

615

A)



B)

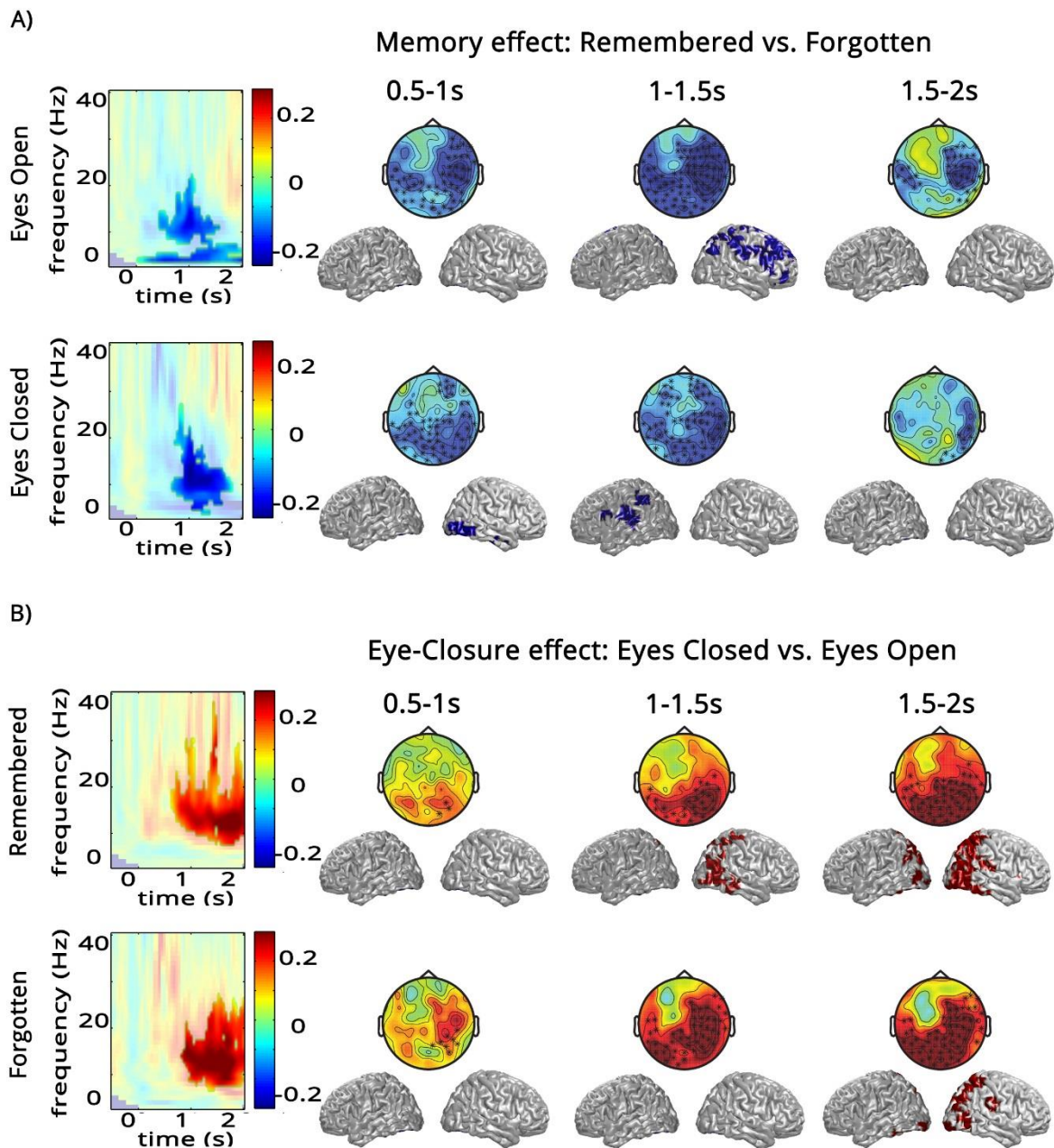


616

617 **Figure 3. A) Grand average time-frequency plot in response to spoken word stimulus and the topography of**

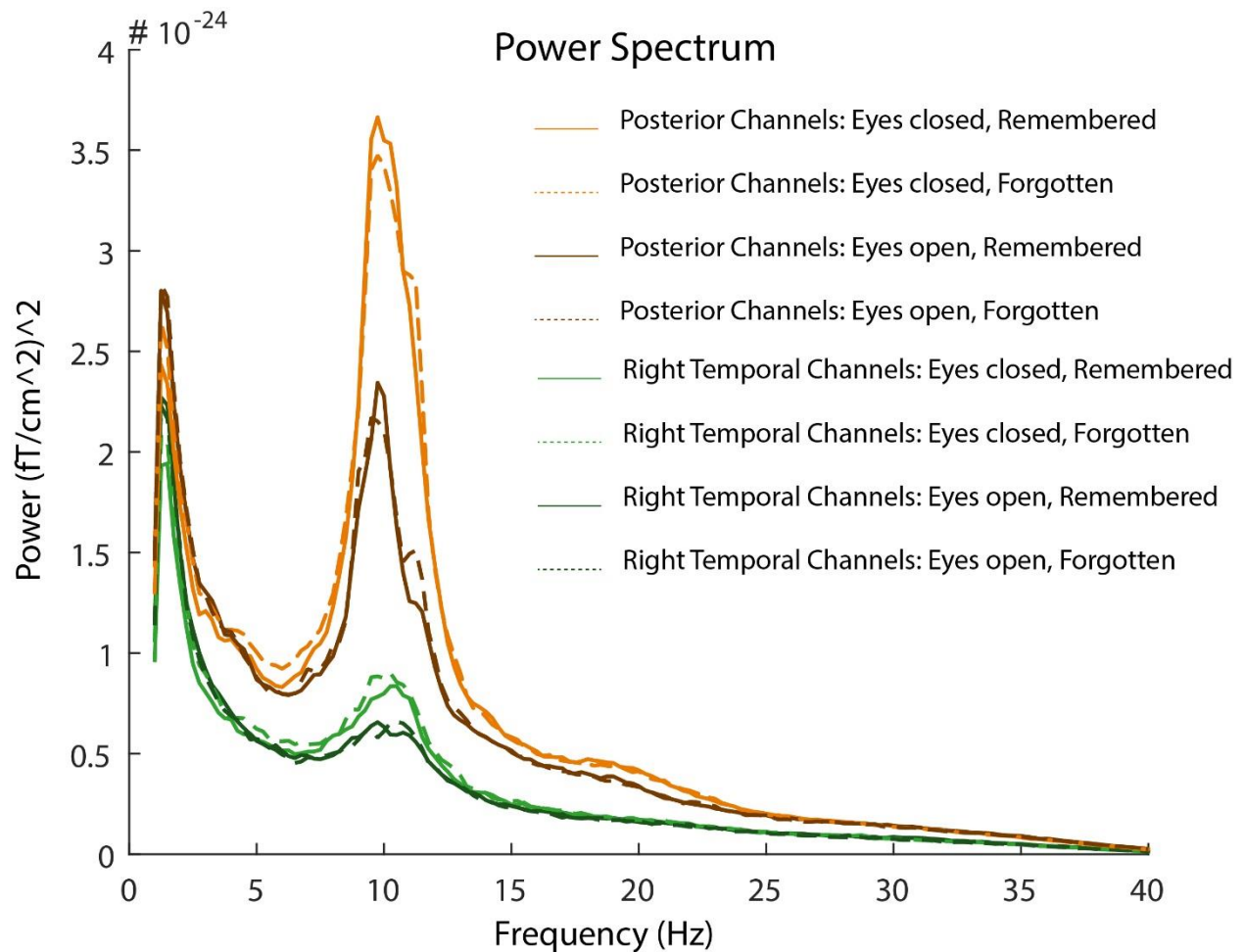
618 **the alpha (7 – 13Hz) ERD between 0.5 and 1 s. B) time-frequency plots in response to spoken word stimulus for**

619 **each of the experimental conditions.**



620

621 Figure 4. Time-frequency plots, topography and source level analysis of the A) Memory effect: Remembered vs.
 622 Forgotten words for eyes open (top row) and eyes closed (bottom row) conditions. B) Eye-closure effect: Eyes closed
 623 vs. Eyes opened for both remembered (top row) and forgotten (bottom row) words. For each row, the time frequency
 624 plot in the left column shows the difference between the two conditions. Opaque colours denote statistically supported
 625 differences. The next three columns show the topography and source localization of these differences for each time
 626 window: (0.5, 1), (1, 1.5) and (1.5, 2) s, respectively. Asterisks in topography plots denote sensors that form part of
 627 the statistically significant cluster. Source localizations only show statistically significant clusters.



628

629 **Figure 5. Power Spectrum analysis. X axis denotes frequency (in Hz) and Y axis power (in (fT/cm²)²). Orangeish**
 630 **and greenish colours illustrate the power spectrum of occipital channels and right temporal channels,**
 631 **respectively. Lighter colours denote eyes-closed conditions, and darker colours represent eyes-open conditions.**
 632 **Dashed lines denote forgotten items and filled lines denote remembered items.**

633

634 **Tables**

Condition	Right Temporal Channels	Occipital Channels	t (p-value)
Eyes closed, Remembered	9.44 (1.60) Hz	9.78 (1.35) Hz	-0.7616 (0.4552)
Eyes open, Remembered	9.50 (1.78) Hz	9.90 (1.44) Hz	-0.8241 (0.4196)
Eyes closed, Forgotten	9.79 (1.43) Hz	9.90 (1.37) Hz	-0.3119 (0.7584)
Eyes open, Forgotten	9.94 (1.54) Hz	9.71 (1.58) Hz	0.5795 (0.5687)
Grand Average	9.76 (1.43) Hz	9.78 (1.49) Hz	-0.0577 (0.9546)

635

636 Table 1: Power Spectrum frequency peak analysis. First column indicates experimental condition. Second and third
 637 columns show the means (standard deviations) of the frequency peaks in right temporal channels and in posterior
 638 channels, respectively. Fourth column shows statistical results t-value(p-value) for the paired t-test between channel
 639 groups.

640

641

Restricted oscillatory analysis of the retrieval phase.

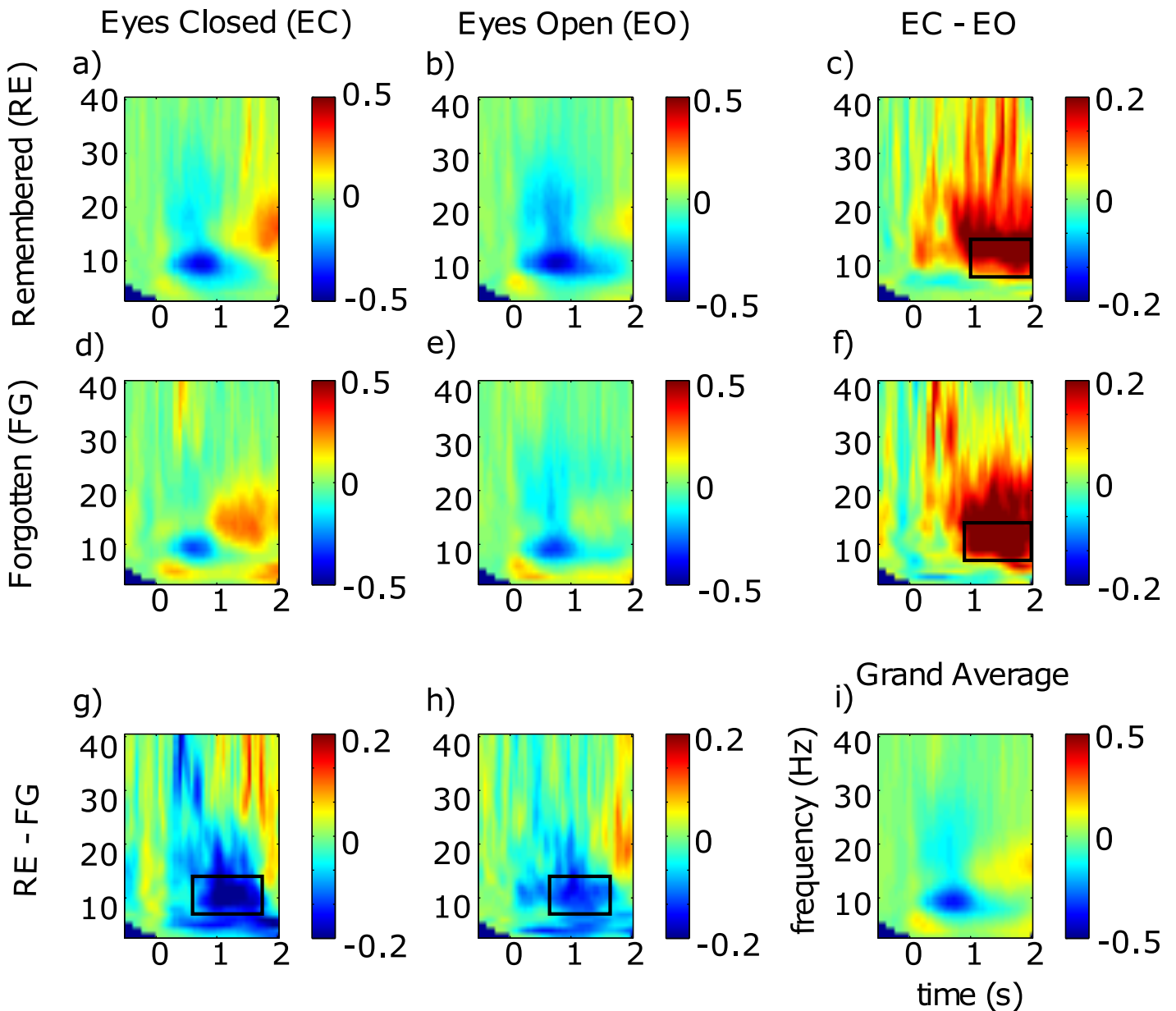


Figure S1. Restricted oscillatory power analysis of the retrieval phase. The power change relative to baseline (-0.5, - 0) s for the retrieval phase as a function of frequency and time. The first row shows power changes for remembered items, and the second row for the forgotten items. The first column shows power changes for eyes closed, and the second column for eyes open. The third row and column show the respective differences across eye closure and item status respectively, and the time-frequency plot on the right bottom corner shows the grand average across items and conditions. Cooler colours denote power ERD and warmer colours denote power ERS.

Topography of alpha band (7 - 13 Hz) power between 0.5 and 1 s.

Freq: 7-13 Hz / Time window: 0.5-1 s

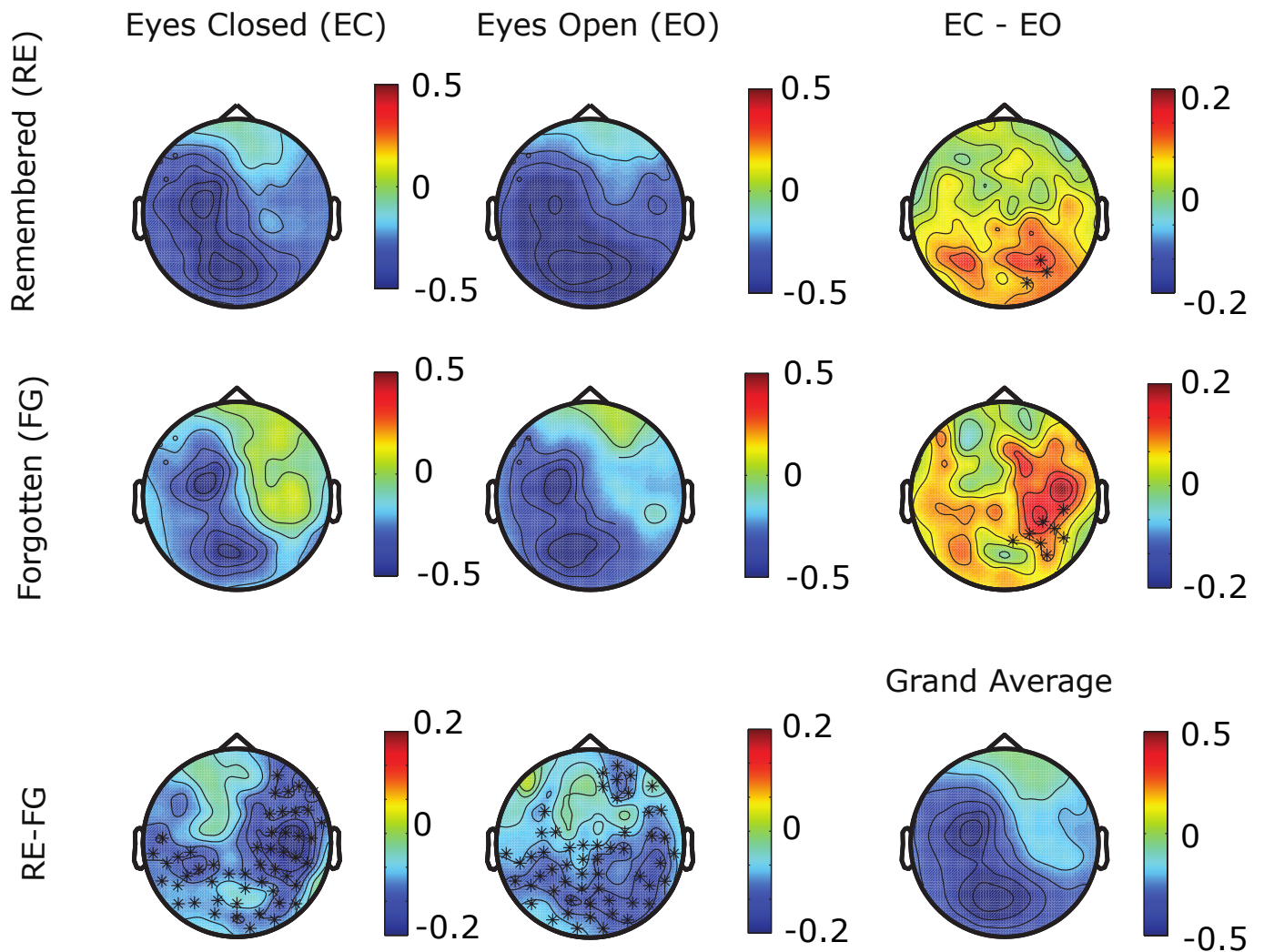


Figure S2. Topography of alpha (7 - 13 Hz) band power between 0.5 and 1 s. The layout of each of these figures is the same layout as Figure 3. Each topography plot shows the relative to baseline power change for the alpha band (7 - 13 Hz) over combined planar gradiometer sensors. The bold stars denote the sensors that were part of the cluster for each comparison. colour scale is the same as in Figure S1.

Topography of alpha band (7 - 13 Hz) power between 1 and 1.5 s.

Freq: 7-13 Hz / Time window: 1-1.5 s

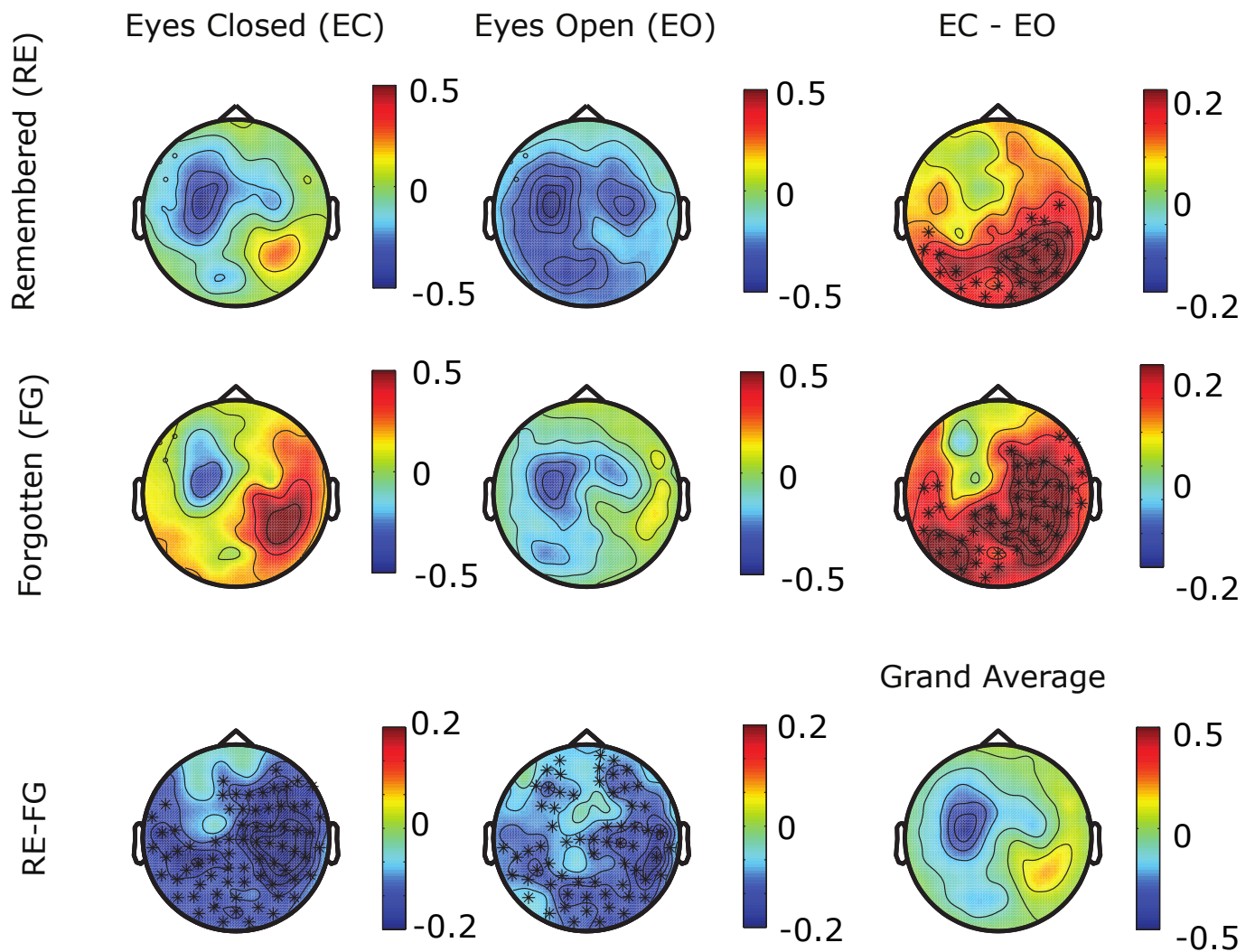


Figure S3. Topography of alpha (7 - 13 Hz) band power between 1 and 1.5 s. Layout is similar to S2.

Topography of alpha band (7 - 13 Hz) power between 1.5 and 2 s.

Freq: 7-13 Hz / Time window: 1.5-2 s

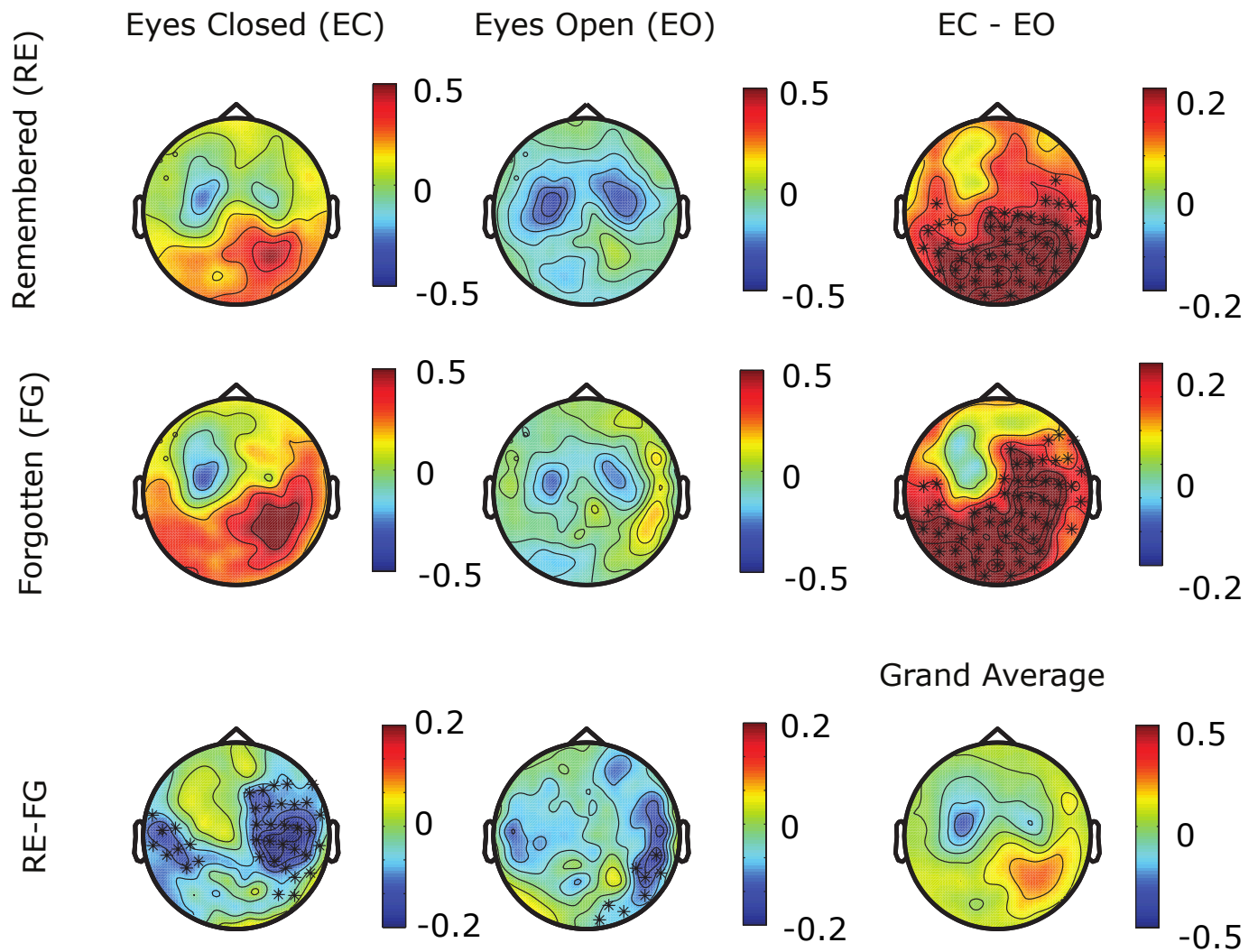


Figure S4. Topography of alpha (7 - 13 Hz) band power between 1 and 1.5 s. Layout is similar to S2.

Unrestricted oscillatory analysis of the retrieval phase.

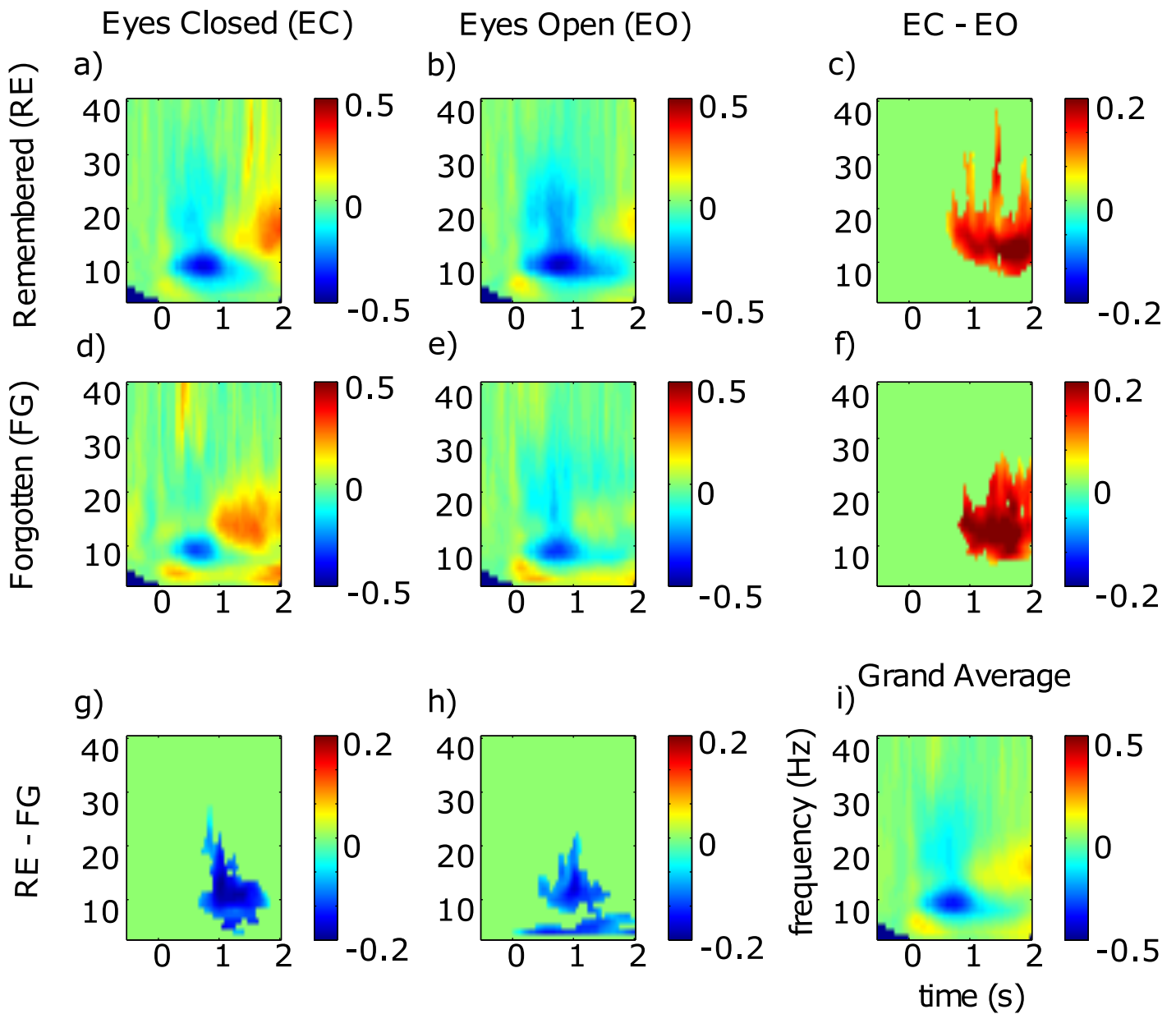


Figure S5. Unrestricted oscillatory power analysis of the retrieval phase. Layout is similar to Figure S1. Plots (c),(f),(g) and (h) show only the time-frequency points that were part of a cluster with statistical support.

Topography of alpha band (7 - 13 Hz) and beta band (13 - 30 Hz) between 0.5 and 1 s.

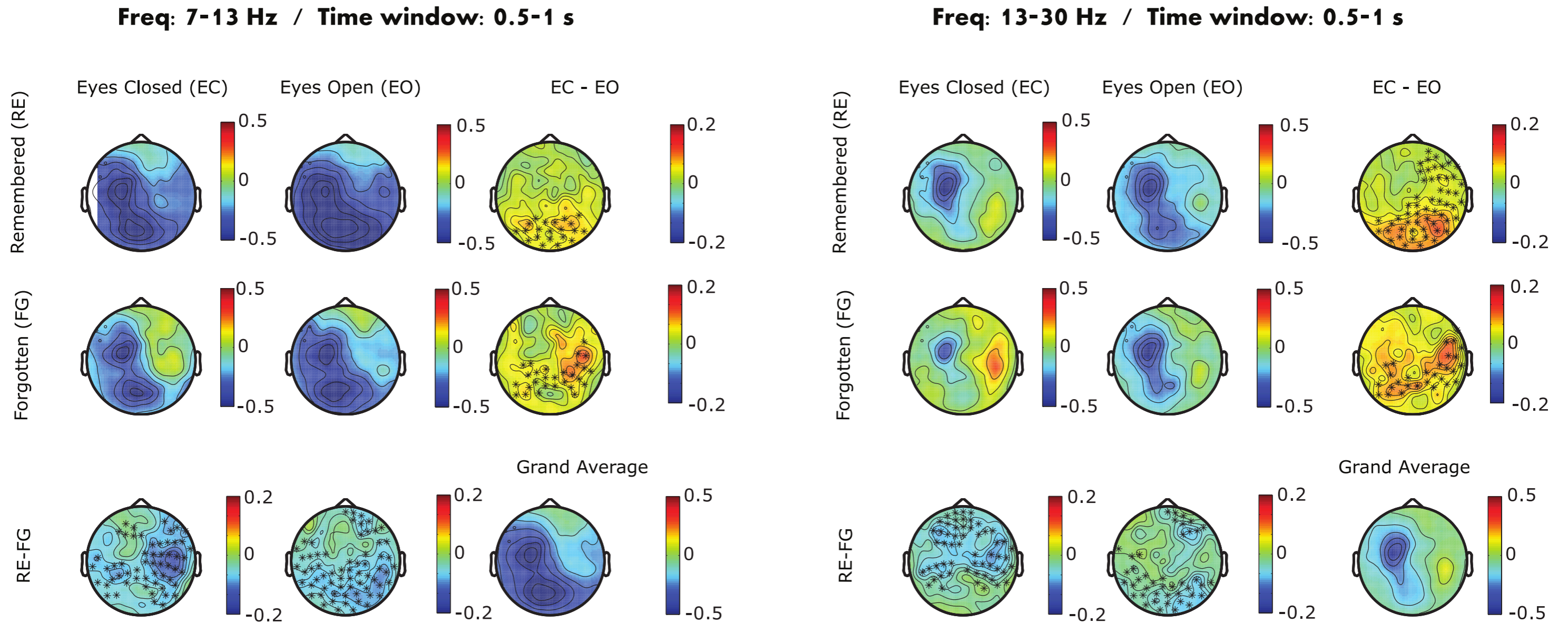


Figure S6. Topography of the relative power changes for alpha (7 -13 Hz) and beta (13 - 30 Hz) between 0.5 and 1 s. The left layout (a) shows alpha band (7 - 13 Hz) power. The right layout (b) shows beta band (13 -30 Hz) power. In each layout, first row represents the remembered items, and the second row the forgotten items. The first column, represents the eyes closed conditions and the second the eyes open condition. The third row and column show the respective differences, and the topography plot on the right bottom corner shows the grand average across items and conditions.

Topography of alpha band (7 - 13 Hz) and beta band (13 - 30 Hz) between 1 and 1.5 s.

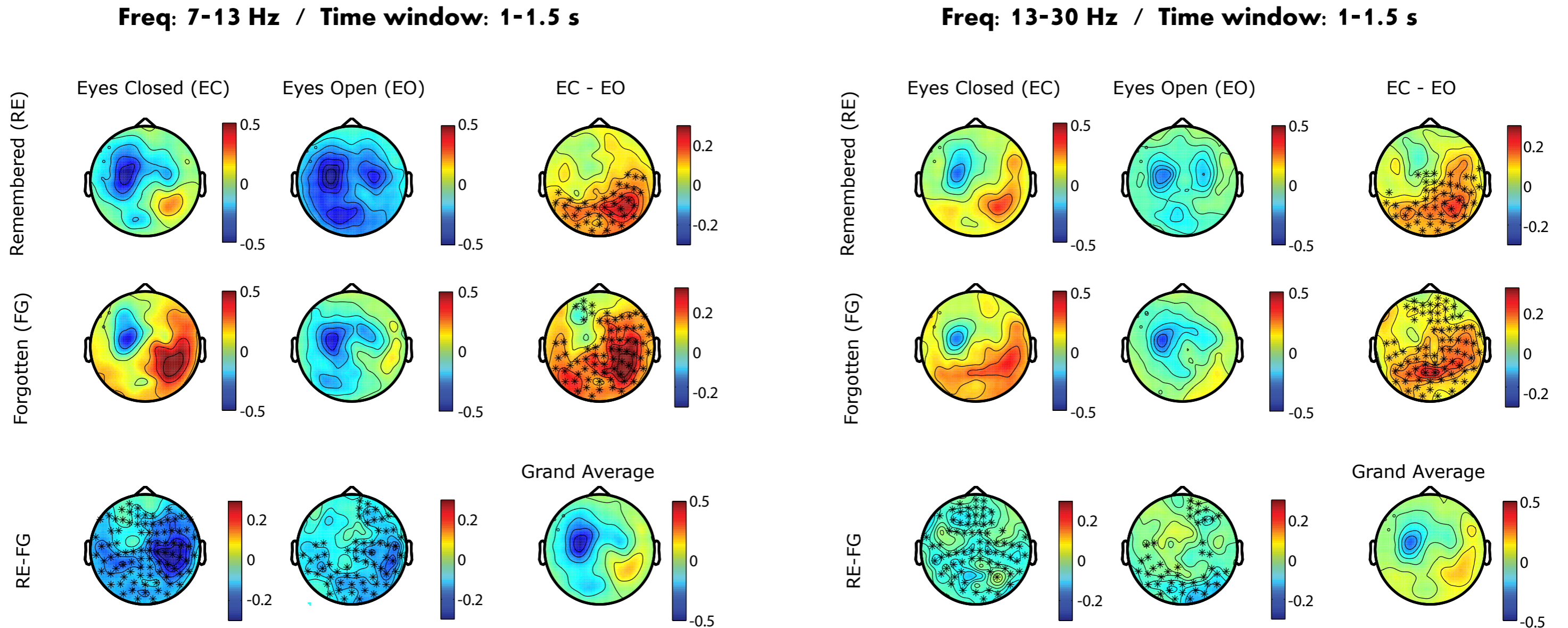


Figure S7. Topography of the relative power changes for alpha (7 -13 Hz) and beta (13 - 30 Hz) between 1 and 1.5 s. The layout is the same as Figure S6.

Topography of alpha band (7 - 13 Hz) and beta band (13 - 30 Hz) between 1.5 and 2 s.

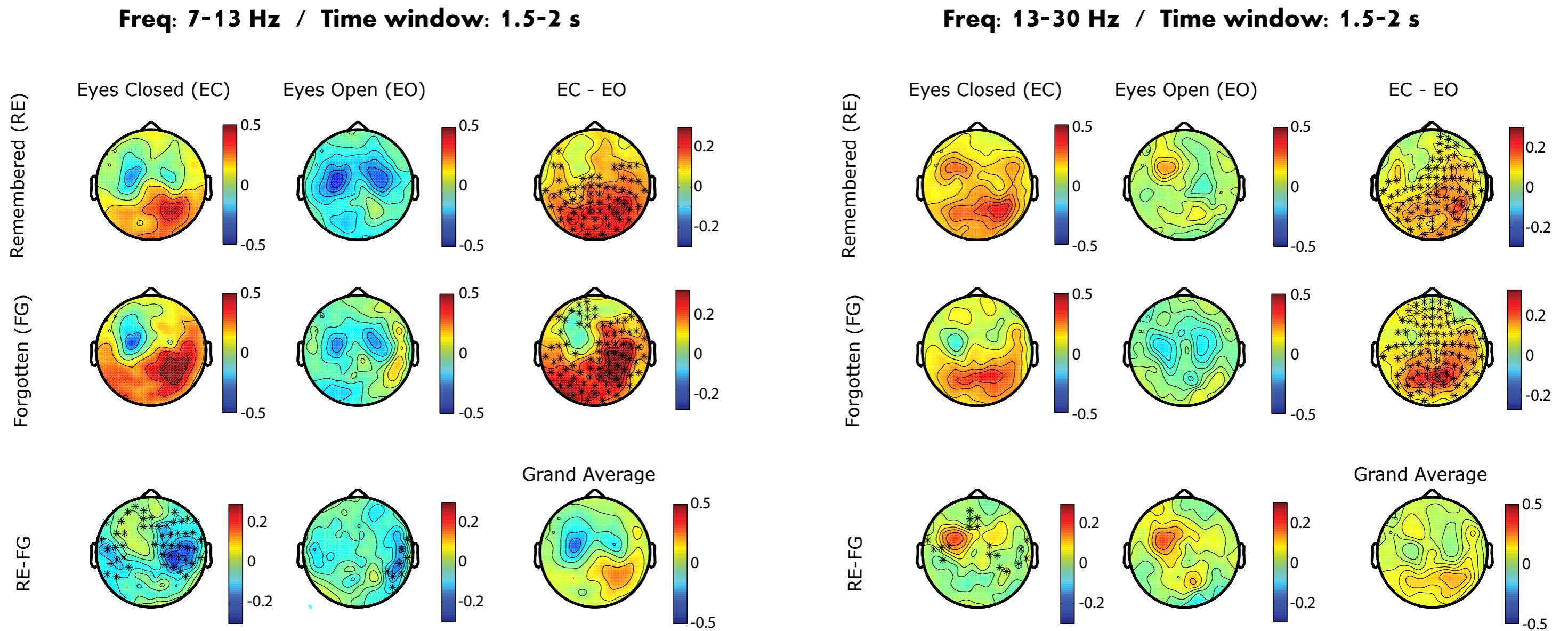


Figure S8. Topography of the relative power changes for alpha (7 - 13 Hz) and beta (13 - 30 Hz) between 1.5 and 2 s. The layout is the same as Figure S6.

Source reconstruction for alpha (7 -13 Hz) between 0.5 and 1 s.

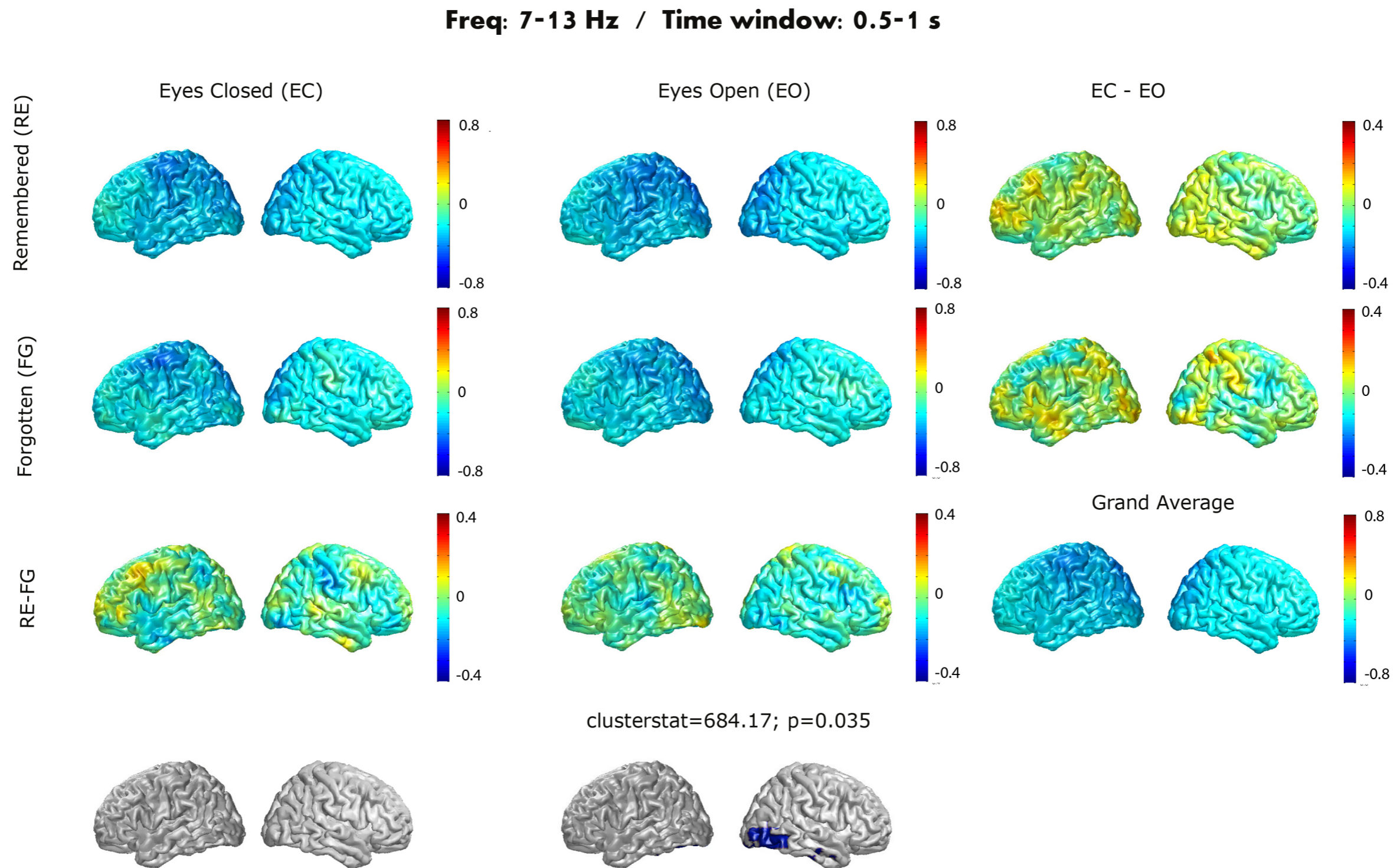


Figure S9. Source reconstruction for alpha (7 -13 Hz) between 0.5 and 1 s. Fourth row and column show the localisation of the clusters that statistically show differences between conditions. The layout is the same as Figure S1,

Source reconstruction for alpha (7 -13 Hz) between 1 and 1.5 s.

Freq: 7- 13 Hz / Time window: 1-1.5 s

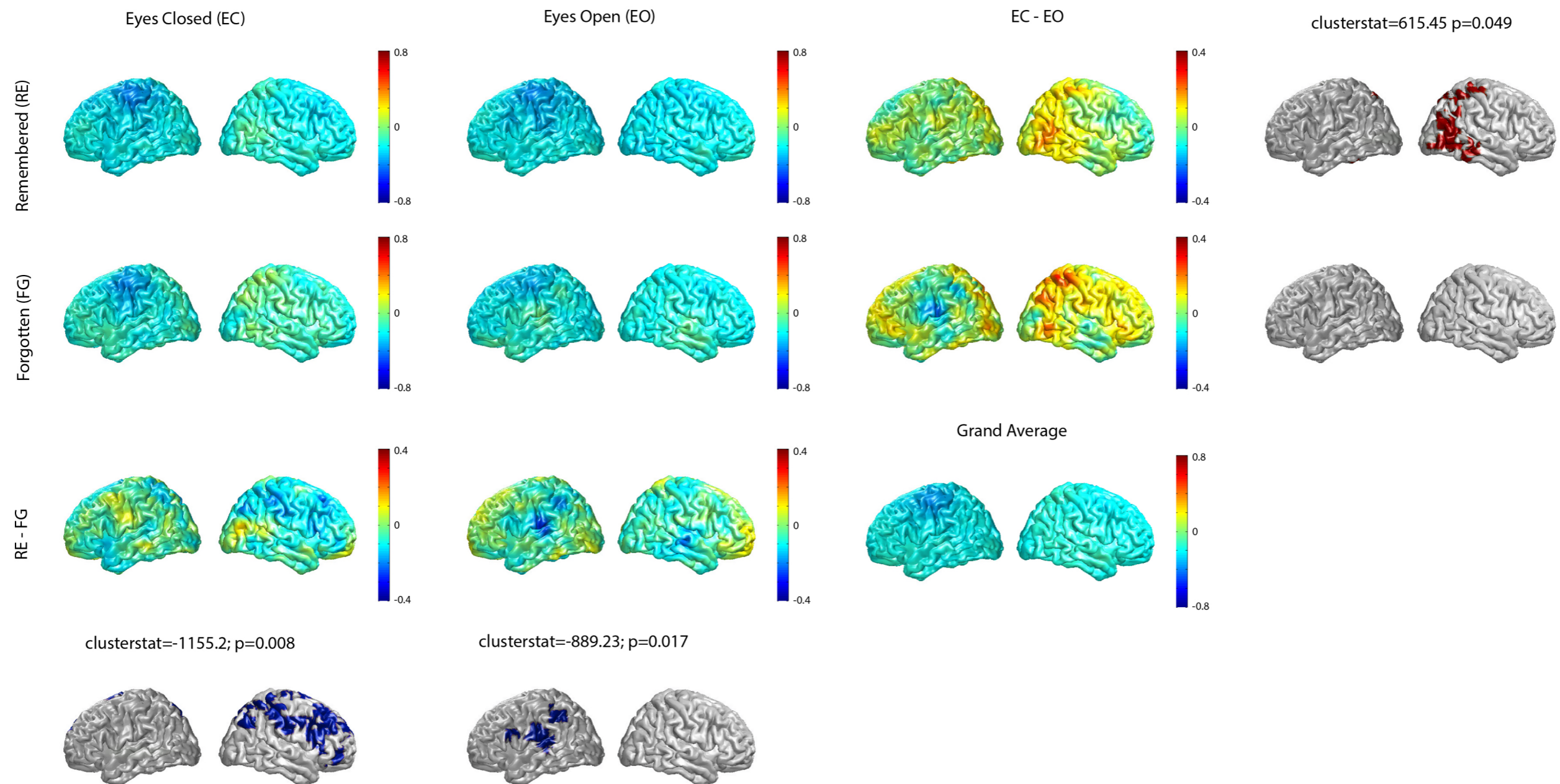


Figure S10. Source reconstruction for alpha (7 -13 Hz) between 1 and 1.5 s. Fourth row and column show the localisation of the clusters that statistically show differences between conditions. The layout is the same as Figure S1.

Source reconstruction for alpha (7 -13 Hz) between 1.5 and 2 s.

Freq: 7-13 Hz / Time window: 1.5-2 s

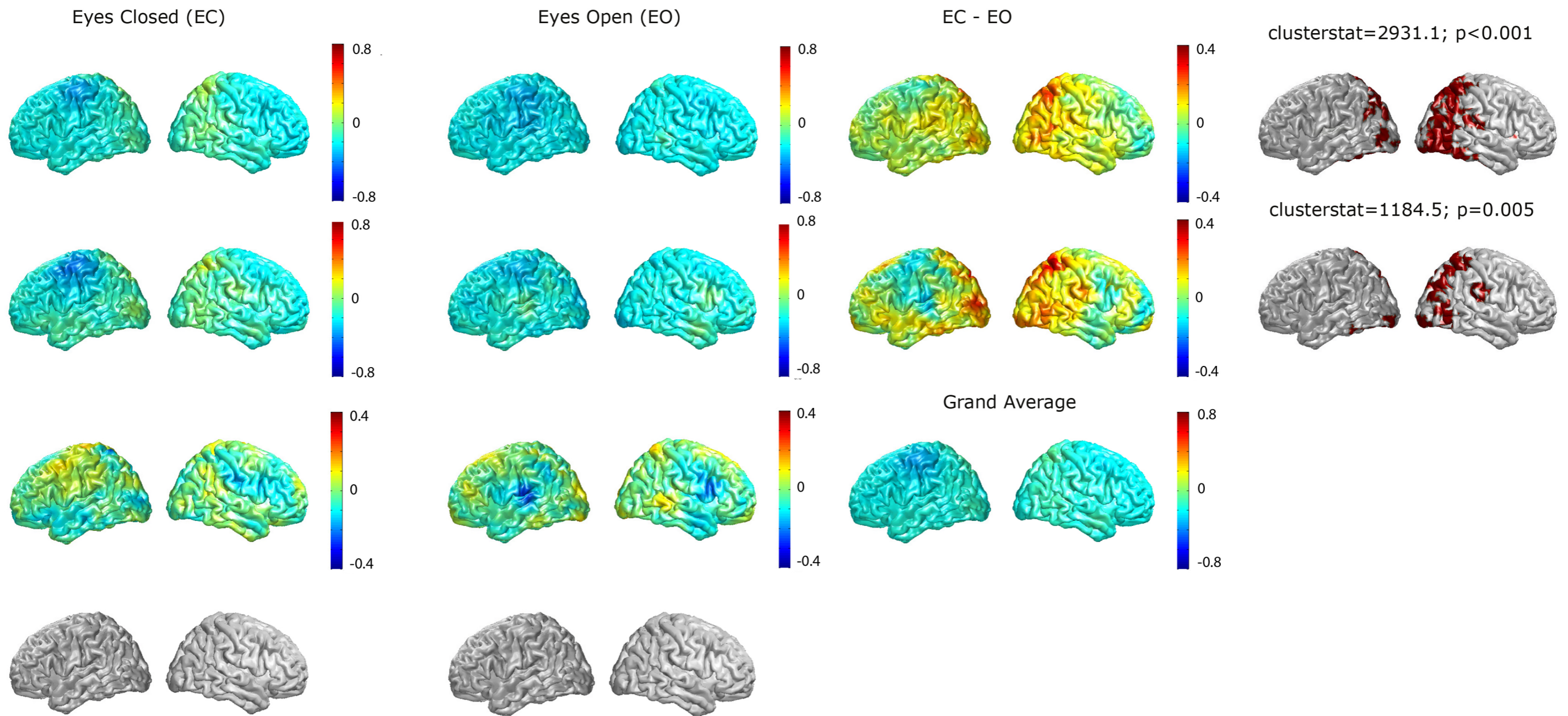


Figure S11. Source reconstruction for alpha (7 -13 Hz) between 1.5 and 2 s. Fourth row and column show the localisation of the clusters that statistically show differences between conditions. The layout is the same as Figure S1,