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Spontaneous alpha brain dynamics track the episodic “when”

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41

42 **Abstract**

43 Across species, neurons track time over the course of seconds to minutes, which may feed the sense of
44 time passing. Herein, we asked whether neural signatures of time-tracking could be found in humans.
45 Participants stayed quietly awake for a few minutes while being recorded with magnetoencephalography.
46 They were unaware they would be asked how long the recording lasted (retrospective time) or instructed
47 beforehand to estimate how long it will last (prospective timing). At rest, rhythmic brain activity is non-
48 stationary and displays bursts of activity in the alpha range (α : 7-14 Hz). When participants were not
49 instructed to attend to time, the relative duration of α bursts linearly predicted individuals' retrospective
50 estimates of how long their quiet wakefulness lasted. The relative duration of α bursts was a better
51 predictor than α power or burst amplitude. No other rhythmic or arrhythmic activity predicted
52 retrospective duration. However, when participants timed prospectively, the relative duration of α bursts
53 failed to predict their duration estimates. Consistent with this, the amount of α bursts was discriminant
54 between prospective and retrospective timing. Last, with a control experiment, we demonstrate that the
55 relation between α bursts and retrospective time is preserved even when participants are engaged in a
56 visual counting task. Thus, at the time scale of minutes, we report that the relative time of spontaneous α
57 burstiness predicts conscious retrospective time. We conclude that in the absence of overt attention to
58 time, α bursts embody discrete states of awareness constitutive of episodic timing.

59

60 **Significance statement**

61 The feeling that time passes is a core component of consciousness and episodic memory. A century ago,
62 brain rhythms called “alpha” were hypothesized to embody an internal clock. However, rhythmic brain
63 activity is non-stationary and displays on-and-off oscillatory bursts, which would serve irregular ticks to
64 the hypothetical clock. Herein, we discovered that in a given lapse of time, the relative bursting time of
65 alpha rhythms is a good indicator of how much time an individual will report to have elapsed.
66 Remarkably, this relation only holds true when the individual does not attend to time and vanishes when
67 attending to it. Our observations suggest that at the scale of minutes, alpha brain activity tracks episodic
68 time.

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83 Introduction

84 Brain rhythms in the alpha range (α : 7-14 Hz) are canonical markers of the level of consciousness in
85 humans (Berger, 1935; Fell et al., 2010; Klimesch, 2012). They represent neural synchronization in
86 spontaneous fluctuations with a period of about 100 ms generated from a variety of neural sources
87 (Steriade et al., 1990; Steriade, 1999; Raichle, 2015; Halgren et al., 2019; Higgins et al., 2021). Due to
88 their omnipresence at rest, α rhythms were postulated to be the internal clock supporting one's awareness
89 of the passage of time (Treisman, 1963, 1984; Kononowicz and van Wassenhove, 2016; van Wassenhove
90 et al., 2019). To date however, whether spontaneous oscillations can predict an individual's experience of
91 the passage of time at the scale of minutes remains unverified (Kononowicz and van Wassenhove, 2016;
92 van Wassenhove et al., 2019). Herein, we re-assess the original *α clock hypothesis* and ask whether bursts
93 of spontaneous α activity keep track of time. This question was motivated by known non-stationarities in
94 brain rhythms challenging the role of neural oscillations in cognition (Steriade et al., 1990; Cole and
95 Voytek, 2017; van Ede et al., 2018), recent description of time cells with long and diverse periods
96 (Pastalkova et al., 2008; MacDonald et al., 2011; Kraus et al., 2015; Issa et al., 2020; Umbach et al.,
97 2020; Aghajan et al., 2022; Cogno et al., 2022; Tsao et al., 2022), and the identification of paradigmatic
98 shortcomings in earlier work.

99 The *clock hypothesis* posits that in the absence of external sensory inputs, endogenous oscillatory
100 activity (the pacemaker of the hypothesized internal clock) predicts an individual's estimation of elapsing
101 time (Hoagland, 1935; Treisman, 1963). The *clock hypothesis* was built on the intuition that biological
102 tick signals are steady and reliable enough to keep count of time units, like mechanical clocks periodically
103 mark the passing of seconds. In its neurobiological implementation, the tick of the internal clock would be
104 isomorphic to the period of spontaneous α neural oscillations. Hence, the *α clock hypothesis* made the
105 assumption that neural oscillations are stationary, continuous and steadily persistent over time, i.e. can
106 instantiate pacemaker-like rhythmic activity (e.g. 9–11). Under this assumption, measuring an
107 individual's α peak frequency (iAPF) would be equivalent to assessing the rate of change in time units, a
108 metrical basis for the estimation of time. In a series of experiments, Michel Treisman, the instigator of the
109 *α clock hypothesis*, dismissed this idea (Treisman, 1984): he observed that α oscillations did not behave
110 like regular pacemakers. As is now acknowledged, spontaneous brain rhythms display non-stationarities
111 with “up and down states” of bursting activity over time (Steriade et al., 1990; Jones, 2016; Sherman et
112 al., 2016; Cole and Voytek, 2017; Shin et al., 2017).

113 Herein, we wished to characterize spontaneous α brain activity while participants, quietly awake,
114 were unaware they would have to report how much time had just elapsed. In human research, this can be
115 done using a retrospective timing task, in which participants do not know in advance that time is the
116 experimental factor of interest. Retrospective timing tasks engage episodic memory processes (Michon,
117 1975; Hicks et al., 1976; Block, 1985), and are under-studied for two reasons. First, retrospective timing
118 is most relevant and ecologically valid over longer time scales (seconds to minutes and hours) but this
119 time scale prevents collecting many trials within a single experiment (Grondin, 2010; Chaumon et al.,
120 2022; Balci et al., 2023). Second, and most importantly, a conservative retrospective task tests a single
121 trial per participant to prevent attentional re-orientation to time, which would defeat the purpose of the
122 task. With both these conditions fulfilled, retrospective timing emulates life events – mostly single shot
123 experiences in our episodic landscape – and engage memory mechanisms (Michon, 1975; Hicks et al.,
124 1976; Block, 1985). Herein, we contend that this stringent approach allows addressing the basic building
125 block for the automatic coding for the passage of time, at the minute-scale, in a manner very close to real
126 life situations and comparable to inter-species approaches.

127 Our study is unique for several theoretical and empirical reasons. Neuroimaging studies mostly
128 focus on prospective time, when participants covertly or overtly pay attention to time. Herein, our interest
129 is how the brain codes elapsing time when participants do not *a priori* adopt a cognitive strategy to
130 estimate it. Timing tasks mostly focus on how the temporal statistics of external sensory events are
131 attended to, predicted, analyzed, or categorized; herein, we ask how elapsing time in the absence of
132 sensory stimulation is encoded. Thus, we assess how endogenous processes during resting-state (Raichle,
133 2015) contribute to the retrospective sense of time constitutive of the episodic “when” (Friedman, 1993;
134 Buhusi, 2019; Sugar and Moser, 2019). Last, timing tasks typically address short time-scales that are
135 below a few seconds with a repeated number of trials time-locked to stimulations (Busch and VanRullen,
136 2010; Hanslmayr et al., 2011; Chakravarthi and VanRullen, 2012; Jensen et al., 2012; Landau and Fries,
137 2012; Grabot et al., 2017, 2021; Nobre and Van Ede, 2018; Mioni et al., 2020). Under these experimental
138 conditions, the assumption that α oscillations are stationary is a fair approximation of the signals. At the
139 longer episodic time scales investigated here, the assumption of stationarity is clearly violated, which
140 motivates the novel characterization of spontaneous α activity we explored in this study.

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142 **Materials and Methods**

143 **Participants**

144 All participants provided a written informed consent in accordance with the Ethics Committee on Human
145 Research at NeuroSpin (Gif-sur-Yvette, France) and in conformity with the Declaration of Helsinki
146 (2018). 63 right-handed participants (27 males; age = 27 years old, +/- 6 years) were recruited for the first
147 study. All had normal or corrected-to-normal vision and were naive as to the purpose of the study. None
148 declared neurological or psychiatric disorders, and none were under medical treatment. Seven participants
149 were excluded *a priori* from the MEG analysis: one participant showed an extreme time estimation
150 (above the interquartile range), four participants showed non-recoverable noisy MEG data and two
151 participants did not comply with the task. Hence, a total of 56 participants (22 males; age = 27 years old,
152 +/- 6 years) were analyzed in the retrospective time task.

153 Out of the 56 participants tested in the retrospective time task, a subgroup of 25 participants
154 performed a prospective duration estimation task: one participant was excluded from the analysis due to
155 an extreme estimation (above the interquartile range) yielding a final sample for the prospective group of
156 24 participants (11 males; age = 26 years old, +/- 5 years).

157 A new group of 26 right-handed participants (12 males; age = 24 years old, +/- 5 years) were
158 recruited for the visual counting experiment. 3 participants were excluded *a priori* from the MEG
159 analysis: one participant showed an extreme time estimation (above the interquartile range), two
160 participants showed non-recoverable noisy MEG data. Hence, a total of 23 participants (11 males; age =
161 25 years old, +/- 5 years) were analyzed in the retrospective dual-task.

162162

163 **Experimental design**

164 In the quiet wakefulness retrospective time experiment (Figure 1a), the experimenter provided
165 participants with the following instructions before the MEG recording: “I will record your brain activity
166 at rest. Please, refrain from moving at all times and keep your eyes open. To help attenuate eye
167 movements, we suggest you fixate on the black screen in front of you.” Following these instructions, the
168 experimenter left the MEG room and waited for participants to state they were ready to start.
169 Unbeknownst to participants, the recordings lasted 2 minutes (min), 4 min or 5 min. From the
170 participant’s viewpoint, the recording unfolded as follows: the French word *début* (“start”) appeared on

171 the screen for 1s followed by a black screen lasting 4 s. A red dot centered on the screen appeared for 500
172 ms after which the screen remained black for 2 min, 4 min, or 5 min. A second red dot appeared on the
173 screen for 500 ms at the end of the experiment. At the end of the MEG recording, the participant was
174 immediately asked to provide a verbal estimate of how much time had elapsed between the two red dots
175 (retrospective time estimate; rTE). In the retrospective time task, this instruction was fully unexpected by
176 participants, as confirmed by informal debriefing following the recording.

177 In the quiet wakefulness prospective time task, participants were informed prior to the MEG
178 recording that they would be asked to provide an estimation of how much time had passed between the
179 two red dots (prospective time estimate; pTE). These recordings lasted 2 min or 4 min.

180 In the retrospective time task following a visual counting task, 17 small white visual annulus were
181 presented in the center of the screen for 120 ms each. The inter-stimulus interval varied pseudo-randomly
182 between 7 and 45 s. For instance, one sequence of inter-stimulus-interval would be: 16 s, 5 s, 13 s, 22 s, 8
183 s, 5 s, 39 s, 1 s, 6 s, 7 s, 15 s, 7 s, 45 s, 6 s, 22 s, and 7 s. This task lasted 4 minutes. Participants were
184 instructed to detect and count the random occurrences of the annulus and to report their final count at the
185 end of the recording. The task started and ended with the same red dots, which were used as instructions
186 to the participants in defining the retrospective duration (rTE) they were also asked to estimate at the end
187 of the task.

188 Prior to the MEG recordings, participants' impulsiveness (psychological trait measure) was
189 assessed using the French validated BIS-11 (Stanford et al., 2009). 37 (out of 56 participants) in the main
190 retrospective timing task and 25 (out of 26 participants) completed the questionnaire for the visual
191 counting task.
192

193 Behavioral analysis

194 Participants' retrospective (rTE) and prospective (pTE) time estimations were computed relative to the
195 actual clock time that had elapsed between the two red dots as the ratio between the individual's verbal
196 report and clock time. This provided a relative (hence, unitless) measure of duration estimation allowing
197 the comparison of the 2 min, 4 min and 5 min conditions. To test whether participants significantly
198 overestimated or underestimated the elapsed time, we performed one-sample, one-tailed t-tests of the
199 relative time estimates (rTE and pTE). A one-tailed paired-samples t-test was used to compare the rTE
200 and the pTE of the individuals (N=24) who performed the retrospective and prospective timing task. The
201 coefficient of variations (CV) were typically computed as the standard deviation of the population divided
202 by the means of the population. The performance in visual counting task was computed as the ratio
203 between the count reported by participants and the 17 stimuli effectively shown on the screen.

204

205 MEG acquisition

206 We used a whole head Elekta Neuromag Vector View 306 MEG system (Neuromag Elekta LTD,
207 Helsinki) equipped with 102 triple sensor elements (one magnetometer and two orthogonal planar
208 gradiometers) to record electromagnetic brain activity in a magnetically-shielded-room. The sampling
209 frequency was 1 kHz. A high-pass filter of 0.3 Hz was applied online. Horizontal and vertical electro-
210 oculograms (EOG) and -cardiogram (ECG) were recorded during the session. Participants' head position
211 was measured before each block by means of four head position coils (HPI) placed over the frontal and
212 mastoid areas.

213

214 MEG pre-processing

215 Signal space separation (Taulu and Simola, 2006) was applied to decrease the impact of external noise.
216 MEG data were notch-filtered at 50 Hz to remove the power line noise. Ocular and cardiac artefacts were
217 corrected by rejecting independent component analysis (ICA) components computed for MEG data that
218 most correlated with detected ECG and EOG events. All MEG recordings lasted 2 min, 4 min or 5 min.
219 For the great majority of the analyses, and unless otherwise specified, we used the first two minutes of
220 each dataset so as to conduct the analysis on the full set of participants. In the visual counting task, only
221 the MEG signals outside the evoked responses elicited by the presentation of the annuli was considered
222 for the burst analysis. To do so, 800 ms of signals were removed following each stimulus presentation.
223 The output signals consisted of 18 epochs of unequal length. A total duration of 226 s were used for the
224 MEG analysis in this task.

225225

226 **MEG analysis**

227 *Power Spectrum Density*

228 The continuous resting state recordings were segmented into non-overlapping 5 s epochs to compute the
229 power spectrum density (PSD). The PSDs were computed using multitaper between 0.1 Hz and 45 Hz.

230230

231 *Spontaneous alpha localizer*

232 A cluster-based analysis was performed to localize the significant sensors in the α range (7-14 Hz)
233 separately for the magnetometers and the gradiometers. In the main text, we report results for the
234 magnetometers for simplicity and refer to them as “sensors”. All outcomes of our analyses could be
235 otherwise be replicated for gradiometers. For a complete report and replication, Figure 1-1 and 1-2
236 provide outcomes of the main findings for the gradiometers.

237 On a per individual basis, the 1/f trend of the PSDs was compensated for in each epoch and
238 sensor. For this, we computed the mean PSD per sensor and normalized them by the grand mean PSD
239 taken over all sensors. To localize sensors most sensitive to α , we ran a cluster-based permutation analysis
240 (Maris and Oostenveld, 2007) implemented in MNE-Python (Gramfort et al., 2013) by drawing 1000
241 samples for the Monte Carlo approximation and using FieldTrip's default neighbor templates for the
242 vectorview MEG system (Oostenveld et al., 2011). The randomization method identified the MEG
243 sensors whose statistics exceeded a critical value, with neighboring sensors exceeding the critical value
244 defining the significant cluster. The p-value was estimated based on the proportion of the randomizations
245 exceeding the observed maximum cluster-level test statistic. The cluster-forming threshold was set to
246 .0001, which was equivalent to a t-threshold of 4.2 in an experimental design using 56 participants. Only
247 clusters with corrected p-values < .05 are reported. Robust clusters of 39 magnetometers and 71
248 gradiometers were found.

249249

250 *Spectral analysis and individual alpha peak (iAPF) detection*

251 The FOOOF algorithm3 (version 1.0.0) was used to parameterize neural power spectra (Donoghue et al.,
252 2020). Settings for the algorithm were as follows: the peak width limits were set to [1.0, 8.0], the maximal
253 number of peaks was set to 6, the minimum peak height was set to 0.1, the peak threshold was set to 2.0
254 and the aperiodic mode was fixed. The PSDs of significant sensors were used as FOOOF algorithm input.
255 The algorithm outputs an estimate of the individual α peak frequency (iAPF) and power. The iAPF was
256 defined as the local maximum within the frequency range of 7 to 14 Hz, and averaged across significant
257 sensors on a per individual manner (Fig. 1d-e, Fig. 1g-h, Fig. 3g, Fig. 4b). Hence, α power was the

258 average periodic power at iAPF across significant sensors. The median absolute error for iAPF estimation
259 was between 0.1 Hz for low noise and 1.25 Hz for high noise.

260260

261 *Oscillatory bursts analyses*

262 The cycle-by-cycle time-domain analysis was used to detect α oscillatory bursts in the continuous MEG
263 recordings and to quantify each oscillatory cycle amplitude (Cole and Voytek, 2019). We ran this analysis
264 for all three tasks on a per individual basis (Fig. 1f, Fig. 1i, Fig. 3h, Fig. 4c). The threshold parameters
265 used to detect episodes with bursts were as follows: amplitude fraction threshold = .2; amplitude
266 consistency threshold = .4; period consistency threshold = .4; monotonicity threshold = .8; and minimum
267 number of cycles = 3. The Neurodspool was subsequently used to quantify the relative burst time (Cole
268 et al., 2019), a feature which indicates how bursty a signal is: 100% means the continuous data was
269 detected as α burst during the entire time (sustained oscillatory signal) whereas 0% means that no α
270 oscillations were found. Relative burst time and burst amplitude were computed for all selected sensors
271 and averaged on a per individual basis. The same procedure was ran on all other canonical frequency
272 bands (Fig. 2d-f). Thresholds for the delta, theta and beta bands were set to: amplitude fraction threshold
273 = 0.3; amplitude consistency threshold = 0.6; period consistency threshold = 0.5; and monotonicity
274 threshold = 0.9.

275

276 *Source estimation of alpha generators*

277 To illustrate the likely cortical generators of the α power, we proceeded with source estimation. The
278 individuals' anatomical MRIs were imported and segmented using the FreeSurfer image analysis suites
279 (<http://surfer.nmr.mgh.harvard.edu/>). A one-layer boundary element model (BEM) surface was generated
280 to constrain the forward model. Individual forward solutions (head models: 10,242
281 icosahedrons/hemisphere; 3.1 mm spacing) were computed using the individual BEM model constrained
282 by the anatomical MRI (aMRI). The aMRI and the MEG were co-registered using the anatomical
283 fiducials (nasion; pre-auricular points; head surface) digitized prior to the MEG acquisition with the
284 MNE-Python suite (Gramfort et al., 2013). To ensure a reliable co-registration, an iterative refinement
285 procedure was used to realign all digitized points with the individual's scalp and was manually checked.
286 We used the noise covariance matrix from one minute of empty room recording prior to the experimental
287 session and used a Linear Constrained Minimum Variance (LCMV) beamforming (Van Veen et al., 1997)
288 approach on the whole brain volume, which estimated the activity of each source at the i^{th} voxel for a
289 given time window. The source estimates were then morphed into a common FreeSurfer average brain
290 (fsaverage) for subsequent group analysis. The activity time courses for each voxel was segmented into
291 non-overlapping 10 s epochs to compute the power spectrum density (PSD). The PSDs were computed
292 using multitaper between 0.1 Hz and 20 Hz, then averaged across all epochs to obtain one PSD per voxel,
293 per individual. Then, we compensated the 1/f trend of the PSDs of each voxel and normalized them by the
294 grand mean PSD taken over all voxels on a per individual basis. The grand-average source estimates
295 across participants for retrospective and for prospective condition are presented in Figure 1-3.

296296

297 *Statistical analyses*

298 In the retrospective time estimations analyses, the rTE, the iAPF, the α power and the relative burst time
299 measurements were all normally distributed as assessed by Shapiro-Wilk's test (rTE $p = .232$, iAPF $p =$
300 $.903$, α power $p = .809$, relative α burst time $p = .156$). However, the assumption of normality was not
301 achieved for the α burst amplitude ($p = .011$). In the prospective time estimations the pTE, the iAPF, the
302 periodic α power, the α burst amplitude, and the relative burst time were all normally distributed as

303 assessed by Shapiro-Wilk's test (pTE $p = .254$, iAPF $p = .980$, α power $p = .909$, α burst amplitude $p =$
304 $.068$, relative burst time $p = .374$). In the visual counting task, the rTE, the iAPF, the periodic α power,
305 the α burst amplitude and the relative burst time were all normally distributed as assessed by Shapiro-
306 Wilk's test (rTE $p = .168$, iAPF $p = .499$, α power $p = .419$, relative burst time $p = .605$).

307 For all normally distributed variables, we performed Pearson correlation (r). For the non-
308 normally distributed α burst amplitude in the retrospective time task, we used Spearman correlation (ρ).
309 For each significant correlation, we performed the Cook's distance measure to ensure the robustness of
310 our results.

311 In the retrospective time analysis, we wished to clarify which of all the predictor variables (α
312 power, α burst amplitude and α relative burst time) was best at accounting for the variability in
313 retrospective time estimates (rTE). For this, we devised a statistical approach that was highly sensitive to
314 the collinearity of the data. First, we orthogonalized the predictor variables using principal component
315 analysis (PCA). Then, we performed a principal component regression (PCR) to select the best (or
316 combination of) PCA predictor(s) explaining rTE. Last, we performed multiple linear regressions to
317 disentangle statistically the best predictor(s) of rTE. Before applying PCA, we observed that the α burst
318 amplitudes were not normally distributed due to two outlier values. Hence, we replaced these two values
319 by the mean of the population: the α burst amplitude was then normally distributed as assessed by
320 Shapiro-Wilk's test ($p = .158$). The initial eigenvalues indicated that PCA1 and PCA2 explained 84% and
321 14% of the variance, respectively. We excluded PCA3, which explained only 3% of the variance. Second,
322 we performed a PCR using PCA1 and PCA2, which showed that PCA1 significantly predicted rTE ($\beta =$
323 0.08 , $t(53) = 3.83$, $p < .001$) whereas PCA2 did not ($\beta = -0.05$, $t(53) = -1.02$, $p = .310$). Hence, we
324 selected PCA1 for the last step. Last, we conducted four independent linear regressions using rTE as
325 dependent variable and α power, α burst amplitude, α relative burst time and PCA1 as predictors. The
326 goodness-of-fit of these four models were assessed using the Akaike Information Criterion (AIC; the
327 lowest the AIC, the better the fit) from which we can conclude that the relative α burst time was the best
328 predictor of rTE (Table 1).

329 To compare the the iAPF, the periodic α power, the α burst amplitude and the relative burst time
330 between retrospective and prospective timing task, we used paired two-sided t-tests.

331331

332 Results

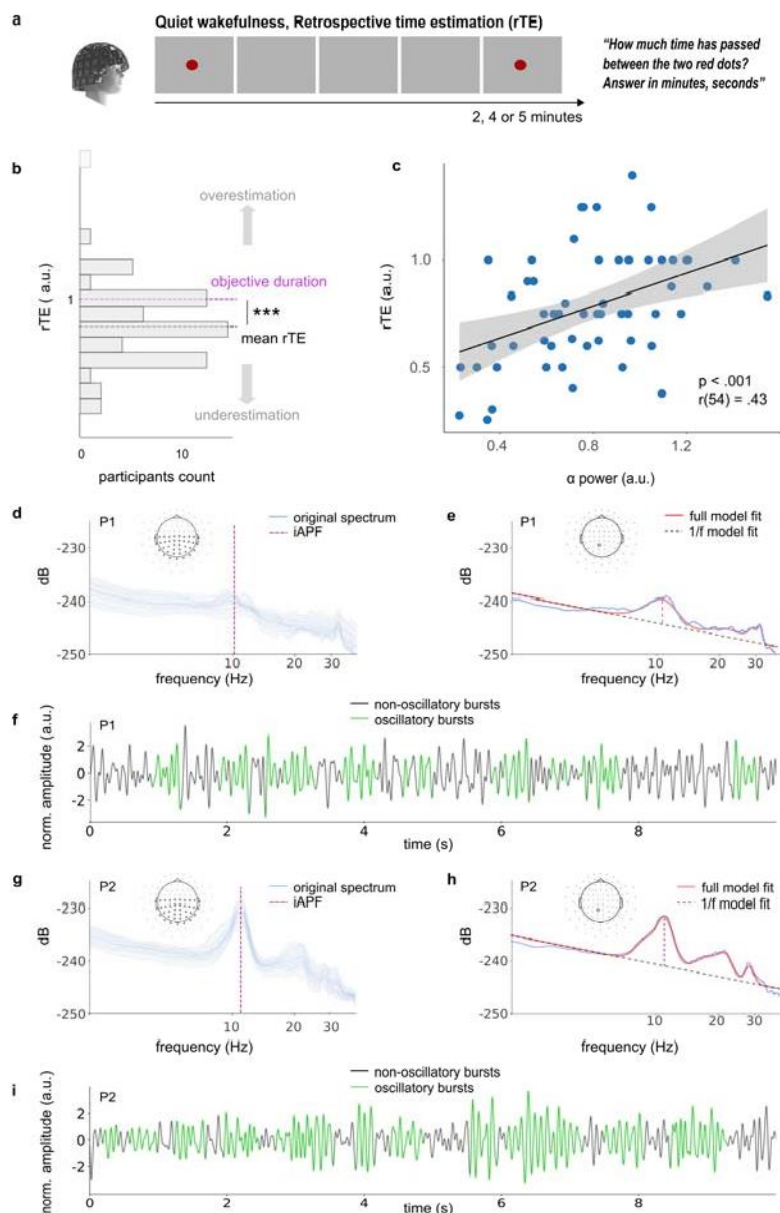
333 In the retrospective time task (Fig. 1a), participants were asked to remain in quiet wakefulness with
334 opened eyes fixating on a screen placed in front of them while being recorded with MEG. A red dot
335 signaled the beginning and the end of the recording, which, unbeknownst to participants, lasted 2, 4, or 5
336 minutes. At the end of the recording, participants were unexpectedly asked to estimate verbally and as
337 precisely as possible (in minutes, seconds) how much time elapsed between the two red dots. We
338 characterized participants' retrospective time estimations as the ratio between their reported duration and
339 the elapsed time (clock duration) to establish a measure of relative retrospective time estimates (rTE). An
340 rTE above 1 indicates that participants overestimated elapsed time, an rTE below 1 indicates that
341 participants underestimated it. On average, participants ($N = 56$) significantly underestimated the duration
342 of their quiet wakefulness during the MEG recording (Fig. 1b; rTE = 0.78 ± 0.26 , $t(55) = -6.1$, $p < .001$).
343 The underestimation of rTE strongly indicates that participants did not pay attention to time (Politi et al.,
344 2018), as a lack of explicit orientation to time would predict and as required by the experiment.

345 One property of duration estimation is its scalar property, in which the variance (σ) of a
346 magnitude estimation increases with its magnitude (μ). As several durations were tested, we computed
347 the coefficients of variation ($CV = \sigma_{rTE} / \mu_{rTE}$) for each and found that, as predicted by scalar timing, the

348 CVs were comparable across durations (Gibbon, 1977) (2 min: $CV = 31\%$, 4 min: $CV = 34\%$, 5 min: CV
 349 $= 35\%$), legitimizing the psychological effectiveness of the retrospective verbal estimations (Chaumon et
 350 al., 2022; Balci et al., 2023).

351 Due to the known relation between impulsivity and timing (Wittmann and Paulus, 2008), we also
 352 tested the correlation between rTE and participants' impulsiveness scores (Stanford et al., 2009). We
 353 found no significant correlations ($\rho(35) = .90, p = .59$) between these two measures, suggesting that rTE
 354 was selective to time estimation and did not reflect an individual's psychological trait.

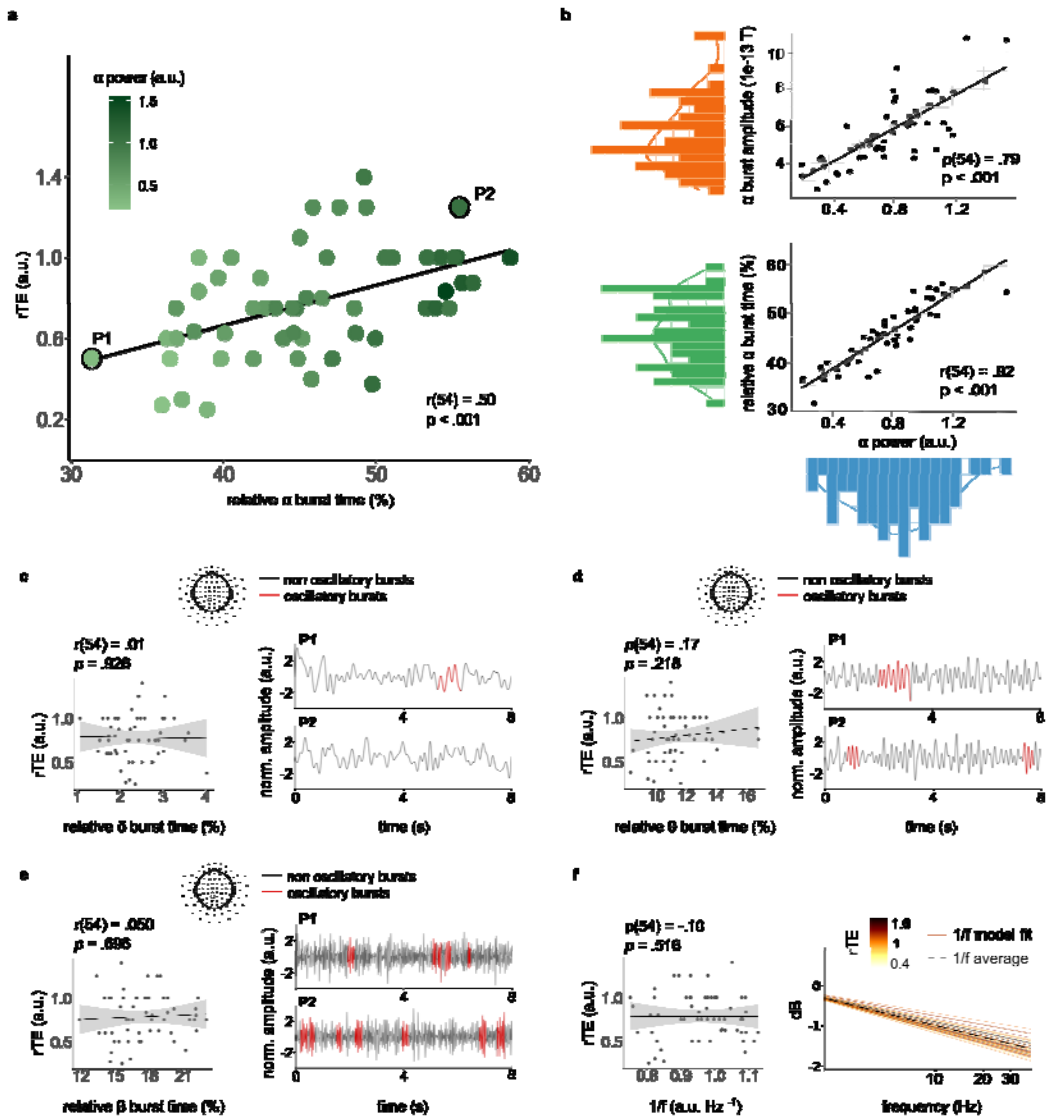
355355



356 **Fig. 1 Retrospective time estimates.** (a) In the retrospective timing task, participants ($N=56$) stayed in quiet wakefulness during
 357 an MEG recording that could last 2, 4, or 5 minutes. Participants received no additional instructions. At the end of the MEG
 358 recording, they were asked to estimate as best they could the duration that elapsed between the two red dots, marking the
 359 beginning and end of the recording. (b) Distribution of the relative retrospective time estimates (rTE) across participants ($N =$
 360 56). The dashed purple line delineates equality between subjective (rTE) and objective (clock) duration. The dashed gray line
 361

362 indicates the mean rTE across participants, indicating that participants significantly underestimated the elapsed time of their quiet
363 wakefulness. The lightest gray bar is an outlier. (e) rTE as a function of α power: stronger α power corresponded to longer rTE.
364 Each dot is a participant. Black line is a regression line and grey shading is 95% CI. Data are reported for magnetometers. Figure
365 1-1 reports the same outcome for gradiometers. Figure 1-2a provides source estimates. (d-i) Data from two representative
366 participants P1 and P2. (d) P1 (rTE = 0.27) showed a flatter distribution of power spectral densities across sensors (blue). The
367 iAPF (dashed purple line) was determined using a spectral model fit *foof* (Donoghue et al., 2020). Figure 1-3a provides iAPF as
368 a function of rTE. (e) Model fit for one sensor (blue) showing the estimated 1/f slope (dashed grey), the full spectral model (red),
369 and the iAPF (purple dashed line). (f). An oscillatory dynamic analysis (cycle-by-cycle) (Cole and Voytek, 2019) was applied to
370 the same sensors to detect and quantify the α burstiness over time (green). (g-i). The same characterization of spontaneous
371 oscillatory dynamics for a second participant P2 (rTE = 1.25). P2 shows stronger α power and α burstiness than P1. *** indicates
372 $p < .001$.

373 We then turned to the individuals' MEG recordings to quantify α activity. We found that stronger
374 α power during quiet wakefulness predicted larger rTE (Fig. 1c and Fig 1-1; $r(54) = .43$, $p < .001$): the
375 larger the α power, the longer the retrospective durations. Given this result, we explored individual's α
376 peak frequency or iAPF (Haegens et al., 2014), which has been implicated in numerous perceptual timing
377 experiments (Samaha and Postle, 2015; Cecere et al., 2017; Minami and Amano, 2017; Ronconi et al.,
378 2018; Mioni et al., 2020). At the scale of minutes, and under the assumption that spontaneous α
379 oscillations are stationary, the *alpha clock hypothesis* would have predicted a positive and linear relation
380 between iAPFs (Fig. 1d-e, 1g-h) and an individual's rTE (Treisman, 1984). However, we found no
381 evidence linking iAPF and retrospective duration estimation ($r(54) = -.10$, $p = .469$; Figure 1-2),
382 suggesting the *alpha clock hypothesis* does not hold as originally conceived.



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384 **Fig. 2 α power and relative α burst time predict retrospective timing.** (a) rTE as a function of the relative α burst time (%),
 385 that is, the relative amount of time α was bursting during the quiet wakefulness period participants estimated the duration of.
 386 Participants' rTE significantly increased with higher relative burst time. Each dot is a participant. P1 (rTE = 0.27) and P2 (rTE =
 387 1.25) are two participants whose spectral dynamics are provided in Fig. 1. Black line is a regression line and grey shading is 95%
 388 CI. Data are reported for magnetometers. Identical outcomes for gradiometers are provided in figure Figure 1-1. (b) Distribution
 389 of α burst amplitude (top panel, orange) and relative α burst time (bottom panel, green) as a function of α power (blue). (c) Left
 390 panel: the relative delta (δ : 1-3 Hz) burst time did not correlate with rTE. Right panel: dynamic oscillatory δ analysis applied to
 391 the data of P1 and P2. (e-f) The same analysis was applied for the theta (θ : 4-7 Hz) and β (15-30 Hz) bands. The relative θ or β
 392 burst times did not significantly correlate with rTE. (h) Left panel: $1/f$ components do not predict rTE. Right panel: comparison
 393 of the $1/f$ components of the average power spectrum across epochs and sensors for each participant. For this, the $1/f$ offset and
 394 exponent per participant were used to reconstruct the aperiodic-only spectrum (Donoghue et al., 2020). Each line shows the
 395 aperiodic spectrum of one participant. The dashed black line shows the mean aperiodic spectrum across participants. The yellow
 396 to brown shading indicates rTE. Figure 2-1 further describes the stability of α burst dynamics over time.

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398 The novel observation that α power linearly correlates with individuals' retrospective duration estimates
 399 relied on time-averaged spectral quantifications, which reduce and impoverish the temporal structure of
 400 brain activity over minutes to a single characterization (i.e. α power). As neural oscillations show

401 burstiness with fluctuating amplitudes, frequencies, and waveform morphologies (Cole and Voytek,
 402 2017), we asked whether the relation between α power and rTE could be better accounted for by the
 403 dynamics of spectral fluctuations. In particular, we questioned whether the relative burstiness of α
 404 rhythms would be a major predictor of elapsing time. Using state-of-the-art analyses (Cole and Voytek,
 405 2019), we detected the presence of α bursts in the MEG data (Fig. 1f, 1i), quantified their amplitude and
 406 the relative time of α bursts during the time interval participants had to estimate (Fig. 2). The relative
 407 burst time indexes the oscillatory dynamics of α activity and ranges from 0 % to 100 %, signifying no-to-
 408 sustained oscillatory α activity, respectively.

409 We found a significant positive correlation between rTE and relative α burst time ($r(54) = .50, p <$
 410 $.001$; Fig. 2a), indicating that the relative duration estimated retrospectively could be predicted by the
 411 relative amount of α bursts in the absence of overt attention to time. This could be predicted as the mean
 412 spectral estimation of α power intuitively fluctuates with both α burst amplitude (Fig. 2b, upper panel)
 413 and relative α burst time (Fig. 2b, lower panel). Interestingly, these relations held true for the entire period
 414 of quiet wakefulness (Fig. 2-1) indicating that α dynamics were stable throughout the experimental
 415 recordings.

416 Given that the different α characterizations are highly collinear, we performed a principal
 417 component regression analysis to establish whether the relative α burst time was a better predictor of rTE
 418 than α power, α burst amplitude, or all of them combined (Table 1). The first principal component
 419 significantly predicted rTE (PCA1: $\beta = 0.08, t(53) = 3.83, p < .001$; PCA2: $\beta = -0.05, t(53) = -1.02, p =$
 420 $.310$) and it was selected for the independent linear regressions using rTE as dependent variable and α
 421 power, α burst amplitude, α relative burst time and PCA1 as predictors. The goodness-of-fit of these four
 422 models were assessed using the Akaike Information Criterion (AIC; the lowest the AIC, the better the fit)
 423 from which we could conclude that the relative α burst time alone was the best predictor of rTE (Table 1).

424

Predictor	<i>p-value</i>	<i>F-value</i>	<i>beta</i>	<i>R</i>	AIC
α relative burst time	< .0001 ***	18.09	.50	.50	-1.20
PCA1 (combination of α power, α burst amplitude and α relative burst time)	< .001 ***	14.62	.46	.46	1.56
α power	< .001 ***	12.50	.43	.43	3.32
α burst amplitude	.016 *	6.23	.32	.32	8.86

425 **Table 1. Model comparisons for the prediction models.** F-values indicate whether the regression model provides a better fit to
 426 the data than a constant value. Beta provides the standardized regression weights. R represents the zero-order correlation. The
 427 Akaike Information Criterion (AIC) was calculated for all models. A lower AIC value indicates a better fit. The α relative burst
 428 time predictor showed the best fit.

429 For theoretical reasons our primary working hypothesis targeted α activity. However, because
 430 different oscillations have been reported in timing tasks (Cravo et al., 2011; Kononowicz and van Rijn,
 431 2015; Kononowicz et al., 2019; van Wassenhove et al., 2019; Herbst et al., 2022), we performed the same
 432 analysis across multiple oscillatory bands (δ : 1-4 Hz ; θ : 4-7 Hz ; β : 15-30 Hz) to test the spectral
 433 selectivity of our findings. Besides α , none of the tested spectral bursts were indicative of rTE (Fig. 2d-e,
 434 δ : $r(54) = -.01, p = .926$; θ : $\rho(54) = .17, p = .218$; β : $r(54) = .05, p = .696$). As the reported activity of
 435 time cells across species spans seconds and minutes (Pastalkova et al., 2008; MacDonald et al., 2011;
 436 Kraus et al., 2015; Issa et al., 2020; Umbach et al., 2020; Aghajan et al., 2022; Cogno et al., 2022; Tsao et
 437 al., 2022), one possibility is that slow-activity building over time would contribute to time estimations.
 438 Slow-activity could be captured as slow aperiodic activity in the spectrum, therefore, we tested whether

439 the aperiodic spectrum or slope of the $1/f$ spectrum - capturing the slowest dynamics in the signals –
440 would show dependency to participants' rTE. We found no such correlations ($\rho(54) = -.10, p = .516$; Fig.
441 2f). Hence, neither the spectral dynamics in other oscillatory regimes, nor scale-free fluctuations showed
442 a significant relation with rTE, supporting that α burst time may be selective to retrospective timing.

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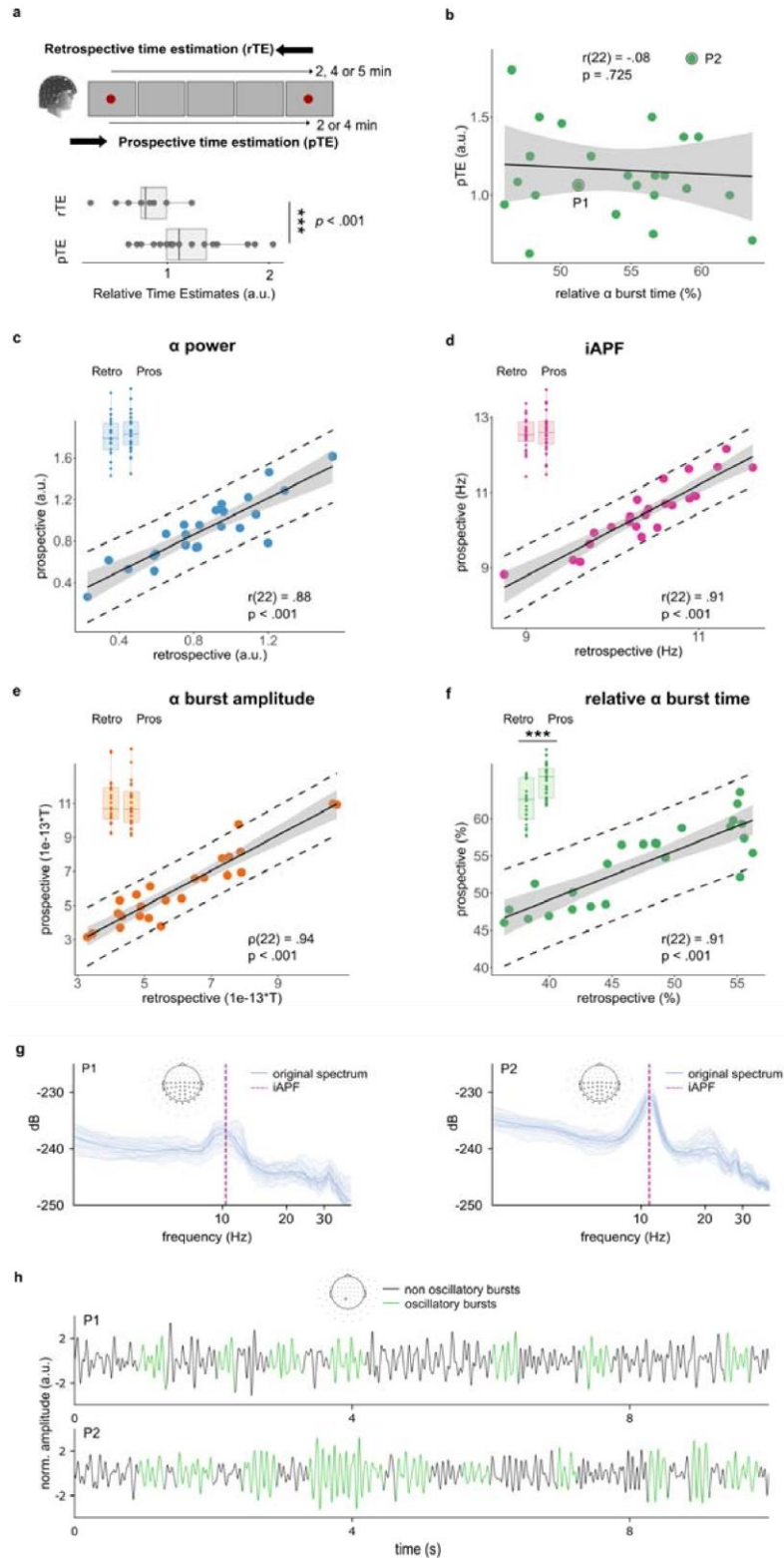
444 We then asked whether the relation between α burst time and retrospective time estimates would
445 hold when participants overtly oriented their attention to time. For this, we collected a prospective timing
446 task in a subset of participants who took part in retrospective time task ($N=24$). We instructed them
447 before the MEG recording to keep track of how much time elapses between the two red dots (Fig. 3a, top
448 panel). We computed the ratio between participants' verbal time estimates and clock duration as relative
449 prospective time estimates (pTE). Participants' pTE showed a significant overestimation of duration spent
450 in quiet wakefulness ($M = 1.20 \pm 0.36$ a.u., $t(23) = 2.75, p = .006$). This outcome was consistent with
451 the fact that attention to time dilates its subjective duration (Brown, 1985; Fortin et al., 2007; Polti et al.,
452 2018). A one-tailed paired samples t-test comparing relative time estimates between the retrospective and
453 prospective tasks showed that participants estimated prospective durations to last significantly longer than
454 the retrospective ones ($t(23) = 4.22, p < .001$; Fig. 3a, bottom panel).

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457 Last, we wondered whether the relation between α burst time and rTE would hold when
458 participants were engaged in a non-timing task instead of being in quiet wakefulness. To test this, we ran
459 another experiment in which naïve participants ($N = 23$) had to count the total number of faint visual
460 stimuli (a total of 17 events) presented on the screen during the MEG recording (Fig. 4a). At the end of
461 the recording, participants were asked to report how many stimuli were detected but also, and
462 unexpectedly for them, to report how much time elapsed between the two red dots. This experiment
463 provides a very stringent control by emulating a more ecologically valid situation in which individuals
464 vacate to occupations distinct from attending to time. Importantly, counting is also known to alter timing
465 (Gaudreault and Fortin, 2013) and α activity is strongly modulated by visual attention (Hanslmayr et al.,
466 2011; Nobre and Van Ede, 2018). Thus, this control task altered both a cognitive and a
467 neurophysiological factor largely predicted to affect timing. On average, participants successfully
468 reported the number of visual events (percent correct count = 0.99 ± 0.11). As we predicted, participants
469 underestimated the duration of the task (rTE = $0.86 \pm 0.31, t(22) = -2.11, p = .023$; Fig. 4a). We then
470 asked whether their rTE could be predicted by α power, which was the case ($r(21) = .45, p = .031$). We
471 then replicated the relation between rTE and the relative α burst time ($r(21) = .51, p = .013$) (Fig. 4d).
472 These results suggest that despite participants being engaged in a visual counting task, the relative burst
473 time of α dynamics predicted individuals' retrospective timing.

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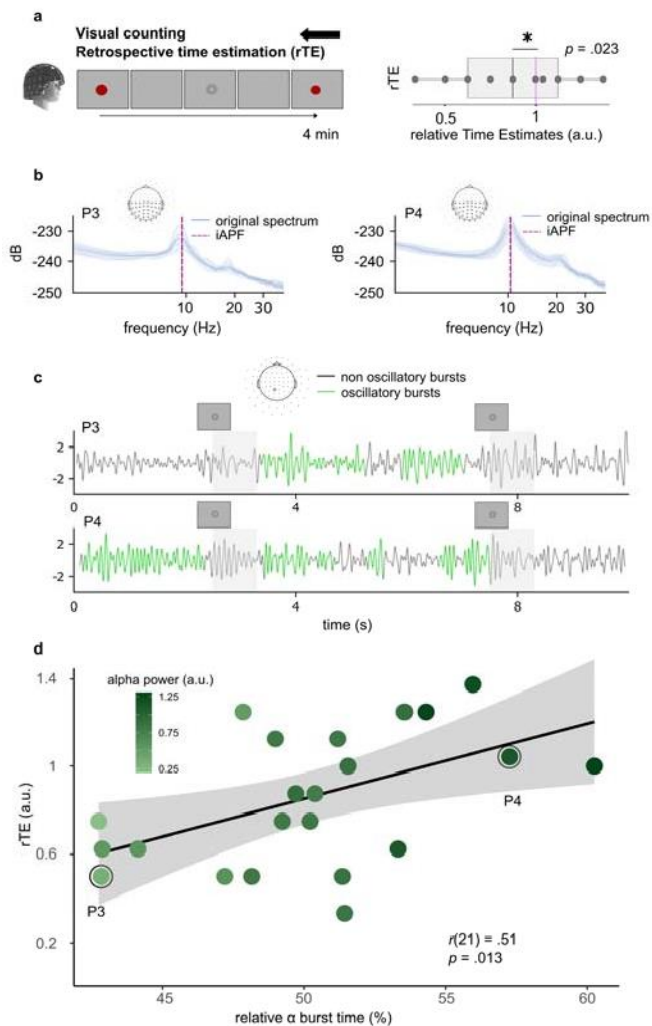


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476 **Fig. 3 Relative α burst time does not predict prospective timing (N = 24).** (a) 24 participants who took part in the
 477 retrospective timing task (rTE) were now asked to estimate the duration that will elapse between the beginning and the end of the
 478 recording (prospective timing, pTE). As predicted, participants estimated the relative duration to be significantly longer in the

479 prospective task compared to the retrospective task. **(b-f)**. Each dot is a participant. Black lines are regression lines and grey
 480 shading are 95% C.I. Retro is retrospective timing data; Pros is prospective timing data. **(b)** The relative duration of α burst
 481 showed no significant correlation with pTE. **(c)** α power (blue) in prospective and retrospective tasks were significantly
 482 correlated and did not significantly differed between the two tasks ($t(23) = -1.73, p = .097$, blue box plots). Figure 1-2a and 1-2b
 483 provides source estimates of α power in the retrospective and prospective conditions, respectively. **(d)** Participants' iAPF
 484 (purple) in prospective and retrospective tasks were highly correlated and did not significantly differed ($t(23) = -1.08, p = .289$;
 485 purple box plots). **(e)** α burst amplitude (orange) in the two tasks significantly correlated and did no significantly differed ($t(23) =$
 486 $-0.05, p = .960$; orange box plots). **(f)** The relative α burst time (green) in prospective and retrospective timing was strongly
 487 correlated but differed between the two tasks: the relative α burst time was significantly higher in prospective than in
 488 retrospective timing task ($t(23) = -8.80, p < .001$; green plots). Data from participants P1 and P2 recorded during the prospective
 489 timing task are illustrated with **(g)** power spectra and **(h)** oscillatory dynamics. *** indicates $p < .001$.

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 492 **Fig. 4 α power and relative α burst time predict retrospective timing despite a visual counting task (N = 23).** (a)
 493 Participants counted faint visual stimuli displayed at random times on the screen during the MEG recording. No instructions
 494 about timing was provided. Participants performed well on the counting task and retrospectively underestimated the elapsed time.
 495 **(b-c)** Data from two participants (P3 and P4). **(b)** P3 (rTE = 0.33) showed a flatter distribution of power spectral densities across
 496 sensors (blue) as compared to P4 (rTE = 1.04). **(c)** P3 showed fewer oscillatory bursts (green) than P4. To prevent contamination
 497 from the evoked responses elicited by the presentation of visual stimuli, 800 ms were taken out of the burst analysis (shaded
 498 gray). **(d)** rTE as a function of relative α burst time (%). Participants' rTE significantly increased with higher relative burst time
 499 and stronger alpha power, replicating and extending our original observations. Each dot is a participant. Black lines are
 500 regression lines and grey shading are 95% CI.

502 Discussion

503 In this series of experiments, we asked whether dynamic features of spontaneous oscillatory activity can
504 tell time at the scale of minutes. We explored this question when individuals did not orient their attention
505 to time (quiet wakefulness; retrospective estimation and episodic time *stricto sensu*) or when they were
506 asked to estimate time in advance (prospective timing task). We report the relative time of spontaneous α
507 bursting activity during quiet wakefulness and during a visual task is a high predictor of participants'
508 retrospective duration estimates at the scale of minutes. This relation did not hold for prospective timing,
509 in which participants were explicitly told to pay attention to time. Our results suggest that spontaneous
510 mechanisms keeping track of time when the observer is not told to keep track of it (retrospective) may
511 largely differ from those used when the observer intently keeps track of it (prospective).

512 Out of the original studies testing the *α clock hypothesis* and failing to find a direct link with
513 duration perception at the scale of minutes (Treisman, 1984; Kononowicz and van Wassenhove, 2016;
514 van Wassenhove et al., 2019), the early study of Werboff (Werboff, 1962) stands out as being the closest
515 to the current experimental venue. In his study, the author compared the “ α wave-count” as the percentage
516 of time α was present in the EEG signal: individuals with a lower occurrence of α waves underestimated
517 elapsed time as compared to individuals with more α waves. However, participants were tested at a time
518 scale of a few seconds (2s and 8s) with a prospective time task. The methodological standards in 1962 are
519 quite remote from our contemporary ones, making it hard to make a direct comparison with our
520 observations. In fact, like a majority of early empirical efforts using prospective timing (reviewed in (van
521 Wassenhove et al., 2019)), we failed to find direct evidence between spontaneous α rhythms and
522 prospective duration estimation. Attending to time may hinder our ability to capture the endogenous
523 dynamics of an internal clocking mechanism due to the diversity of cognitive strategies deployed by
524 participants to keep track of it. Indeed, a great majority of studies use prospective timing tasks, in which
525 participants pay attention to the temporal statistics of upcoming stimuli (Grondin, 2010; Vataakis et al.,
526 2018; van Wassenhove et al., 2019) engage oscillatory activity for a diversity of sensorimotor and
527 cognitive factors. These may confound processes that are selective to the representation of time *per se*.
528 The retrospective timing tasks used here could be argued to relate to implicit timing (Tsao et al., 2022;
529 Sawatani et al., 2023). Implicit timing tasks typically explore sub-second-to-second temporal scales
530 (Nobre et al., 2007; Nobre and Van Ede, 2018), which are crucial for the structuring of sensory
531 information in perception and temporal expectations. Herein, we explored the time scale of minutes and
532 used a single-trial approach to ensure that participants were not aware of the goal of our study. Thus, no
533 (implicit) temporal learning could take place in this experiment. Our approach is important for time scales
534 that are most relevant to episodic timing and that last several seconds, minutes or hours. Herein, we thus
535 used a minimalist retrospective time task and the implication of α rhythms in episodic time tracking
536 became quite salient.

537 Although our results demonstrate the implication of rhythmic-like activity in episodic timing, we
538 do not interpret these findings as evidence for a direct implementation of the *α clock hypothesis*, at least
539 not in the manner it was initially formulated. Rather, and consistent with an information-theoretic view of
540 time estimation (Hicks et al., 1976; Gallistel, 1990), we suggest that the retrospective estimation of the
541 passage of time by participants is linked to episodic memory (Michon, 1975; Block, 1985; MacDonald,
542 2014) and implemented as a count of bouts of awareness (or “events”) during quiet wakefulness. The *α*
543 *clock hypothesis* presented here is not about counting time *per se*; rather, it is about counting events
544 spontaneously and endogenously instantiated as α burst. It is important that we do not interpret such
545 counting mechanism as an explicit and overt counting process, but as an automatic parsing and time-
546 stamping mechanism of internal events. Such episodic parsing would be most similar to an information
547 theoretic event-based clock model (Gallistel, 1990), which can be reconciled with a symbolic approach of

548 timing in memory (Friedman, 1993) and the possible spontaneous dynamics of timing cells observed in
549 various species (Pastalkova et al., 2008; MacDonald et al., 2011; Kraus et al., 2015; Issa et al., 2020;
550 Umbach et al., 2020; Aghajan et al., 2022; Cogno et al., 2022; Tsao et al., 2022). This hypothesis, aligns
551 well with a recent proposal (Tsao et al., 2022), in that α bursts may instantiate state-dependent network
552 trajectories ultimately feeding episodic time estimation.

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554 During quiet wakefulness, the implication of α rhythms in the regulation of the default-mode
555 network is expected. In combined EEG and fMRI recordings, the coexistence of positive and negative
556 fluctuations of neural networks activity with changes in α synchronization have been reported (Goldman
557 et al., 2002; Laufs et al., 2003; Mantini et al., 2007): increases in α power tend to correlate with an
558 increase BOLD response in thalamic and insular cortices, whereas a decrease in α power co-occurs with a
559 decrease in occipital and frontal regions (Goldman et al., 2002; Laufs et al., 2003). Out of six resting-state
560 networks identified during quiet wakefulness (Mantini et al., 2007), the default mode network (Raichle,
561 2015) and the dorsal attentional network (Fiebelkorn and Kastner, 2020) have shown significant
562 congruence with α power fluctuations (Mantini et al., 2007). If the dorsal attention network (Fiebelkorn
563 and Kastner, 2020) is most readily associated with the functional regulation of visual processing during
564 perception, the default mode network (Raichle, 2015) is mostly involved in endogenous processing.
565 While thalamo-cortical circuitries are important contributors to α activity (Steriade et al., 1990; Steriade,
566 1999; Halgren et al., 2019), a significant implication of hippocampal activity has been reported (Raichle,
567 2015). The presence of α bursts suggest that recurrent state-dependent networks may mediate transient or
568 discrete bursts of neural firing in this frequency range. Consistent with this, α rhythms are coupled to the
569 functional state of the default-mode network (Brookes et al., 2011) and α bursts have recently been
570 associated with memory replay (Higgins et al., 2021). Consistent with the *α clock hypothesis* as an event-
571 based episodic tracking mechanism, a recent study demonstrated that in the absence of sensory
572 stimulation and feedforward inputs, α activity endogenously regulates spontaneous thoughts from which
573 high level conscious features can be decoded including the *where* and *what* content (Xie et al., 2020).

574 While α rhythms are the earliest described oscillations in human brain activity (Berger, 1935),
575 they are notoriously difficult to classify in the taxonomy of neural oscillations drawn from animal
576 neurophysiology (Buzsáki and Draguhn, 2004; Buzsáki et al., 2013). While α rhythms are sometimes
577 compared to theta oscillations seen in rodents, human theta and α rhythms show intriguingly divergent
578 developmental trajectories (Cellier et al., 2021) with the precedence of theta rhythms incrementally
579 dominated by α rhythms at 7-8 years old. In light of our findings, it would be particularly interesting to
580 explore how developmental trajectories of episodic timing may or not follow those predicted by
581 neurophysiology. Additionally, the iAPF increases with age to reach a value stable in adulthood and
582 decreases again in aging (Lindsley, 1939; Scally et al., 2018; Cellier et al., 2021). We did not observe a
583 correlational implication of iAPF in this study, but exploiting a larger range of iAPF across ages or
584 longitudinally may provide reliable insights.

585 Taken together, we propose that a large-scale endogenous regulation of α burst activity may
586 contribute to the internal counting of events and bouts of conscious moments, which may support time
587 keeping mechanisms for the individual's episodic *when*. Given the simplicity of our experimental
588 protocol, we believe that this novel *α clock hypothesis* could be tested in a large range of healthy and
589 clinical population and could provide a neural marker for the passage of time. We interpret our findings as
590 suggesting that in the absence of attention to time and temporal task demands, α bursts may embody
591 discrete states of awareness like timestamps in our episodic landscape, from which accurate duration
592 estimates can be recollected retrospectively, in the individual's future.

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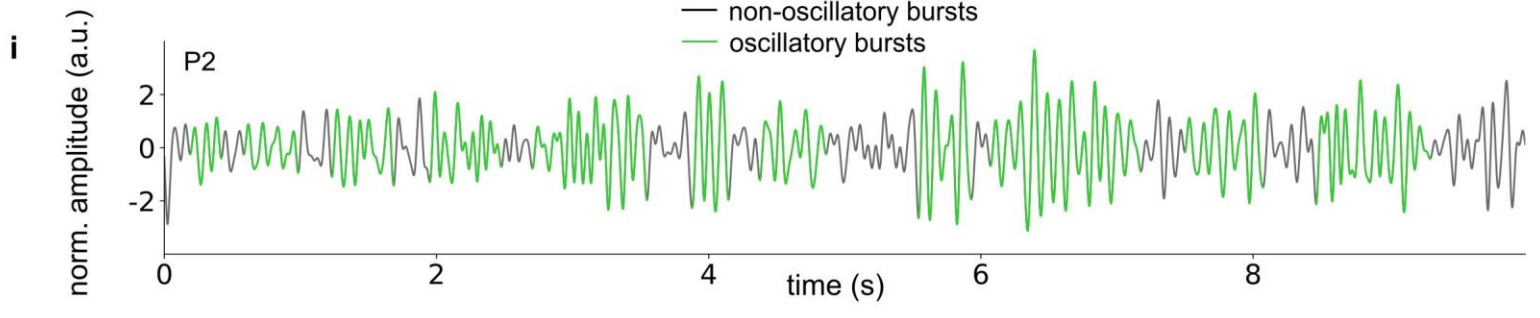
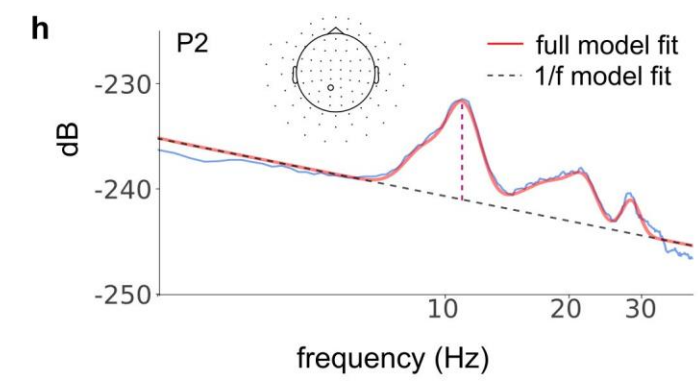
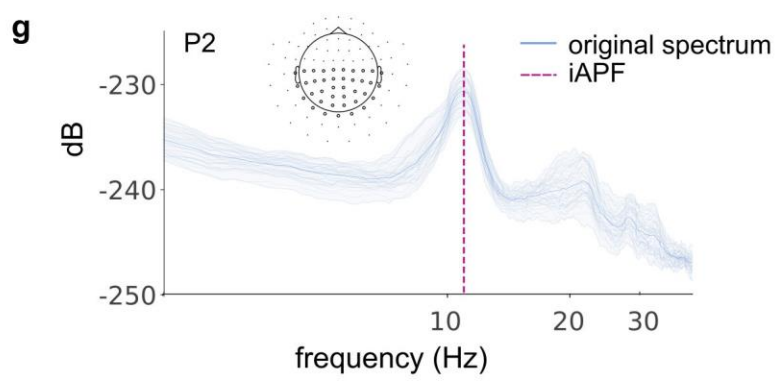
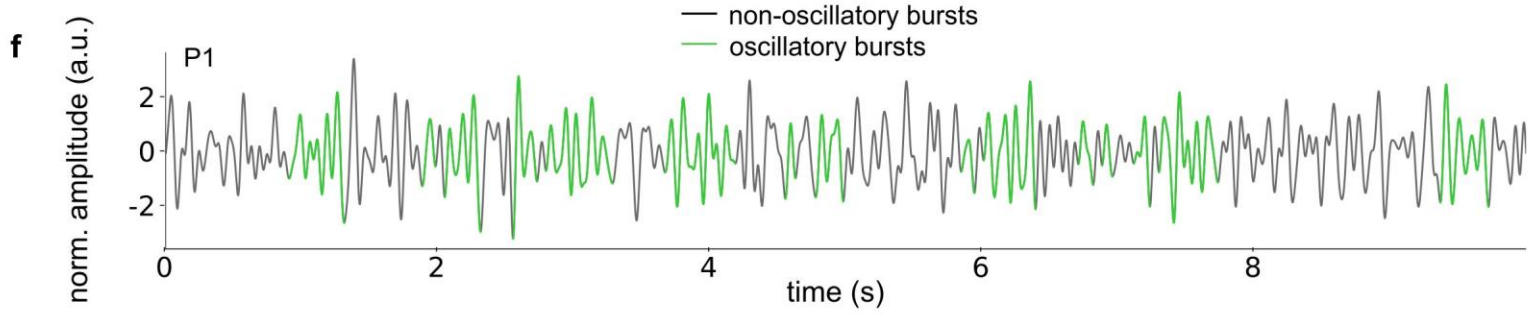
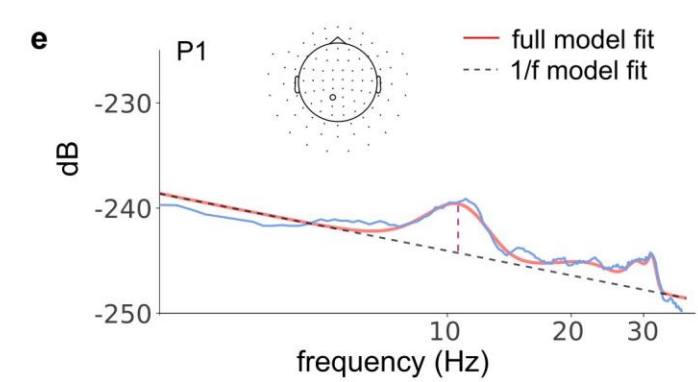
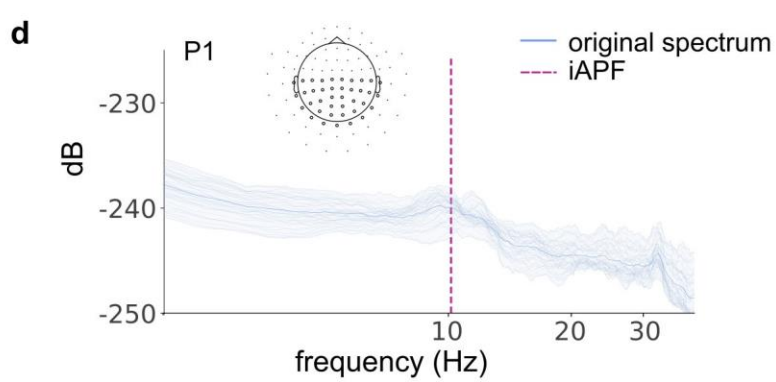
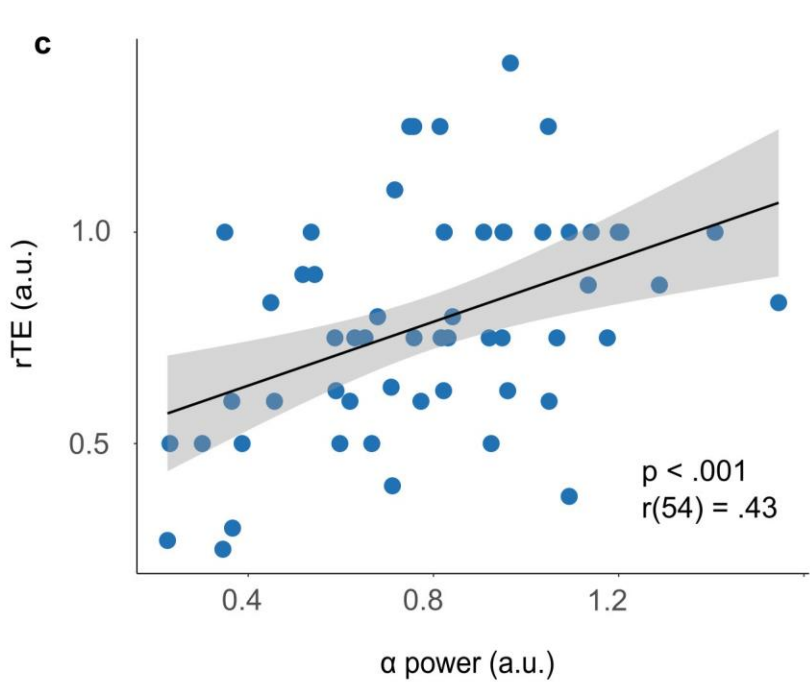
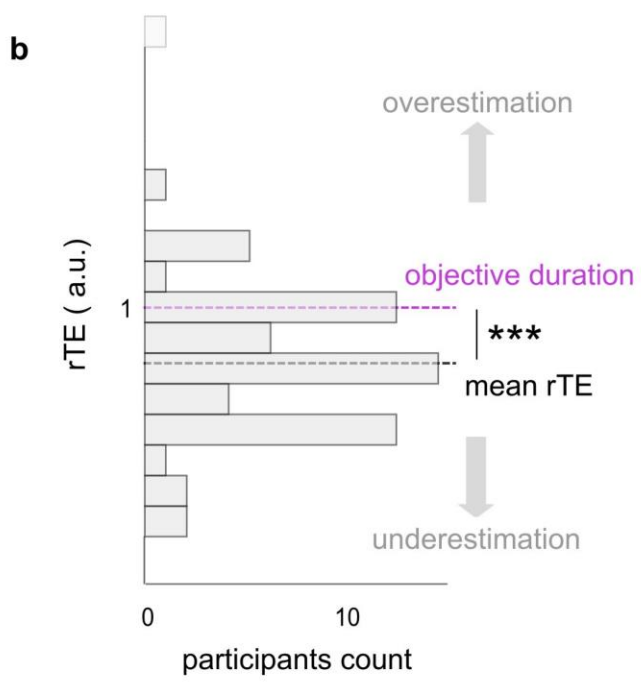
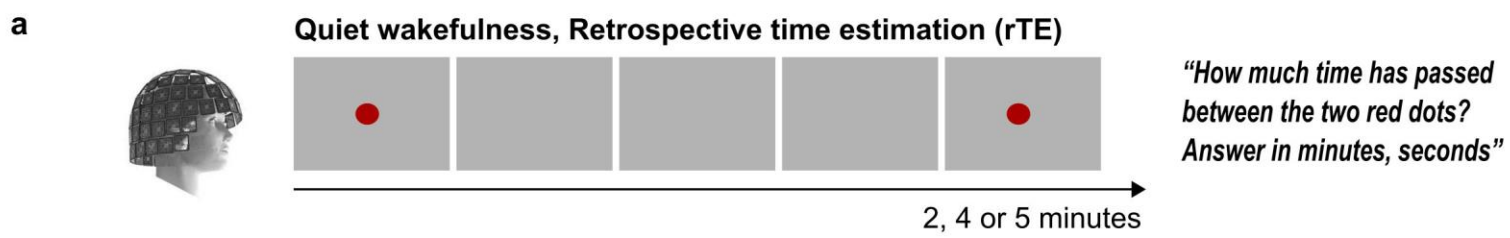
775 **Extended Data**

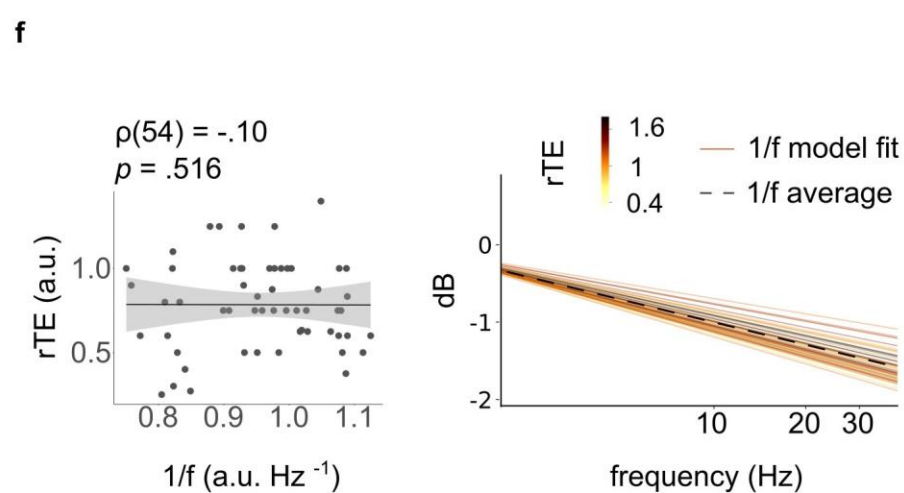
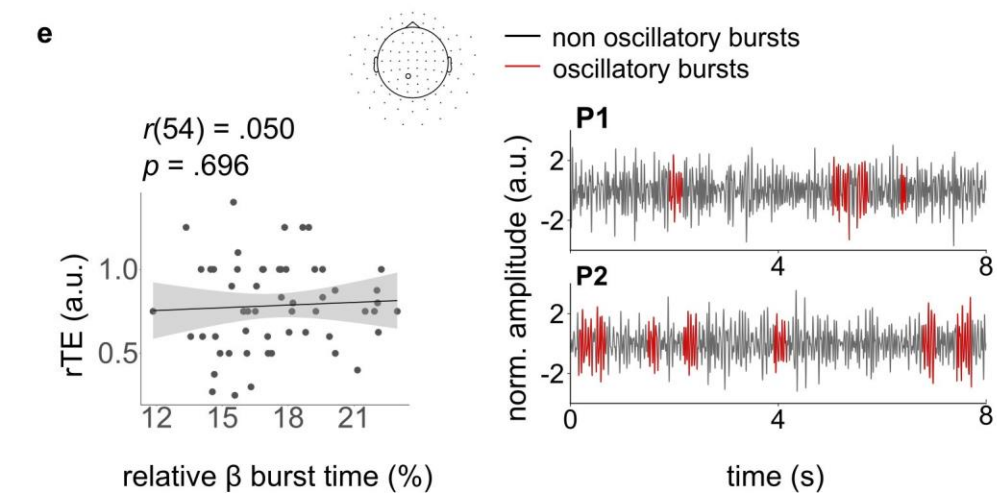
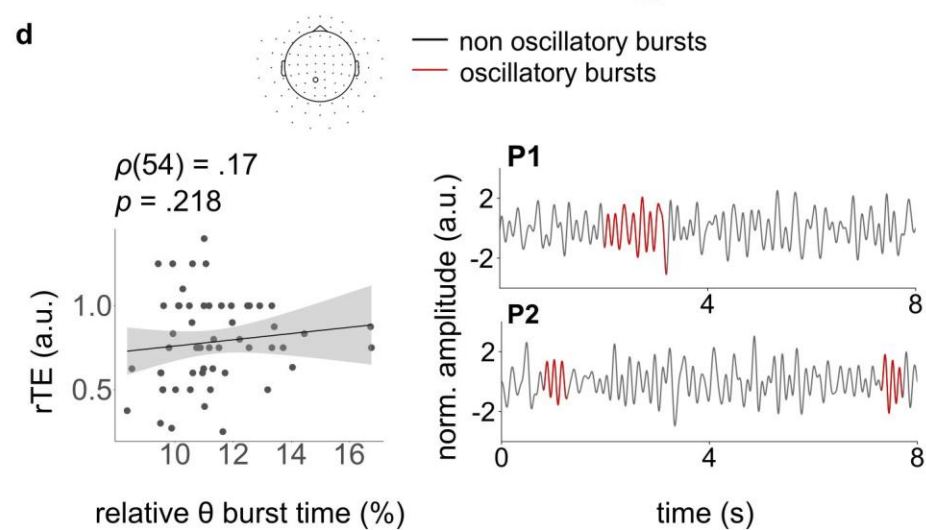
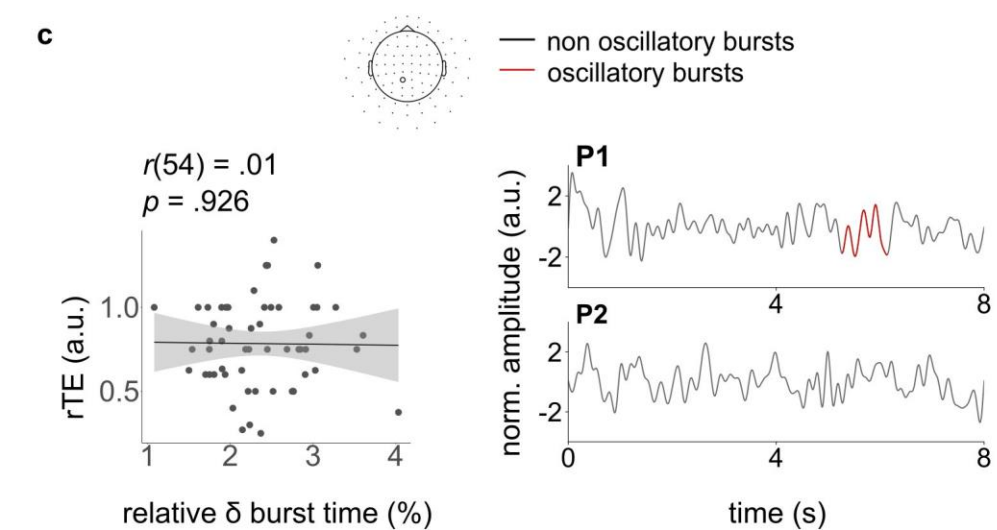
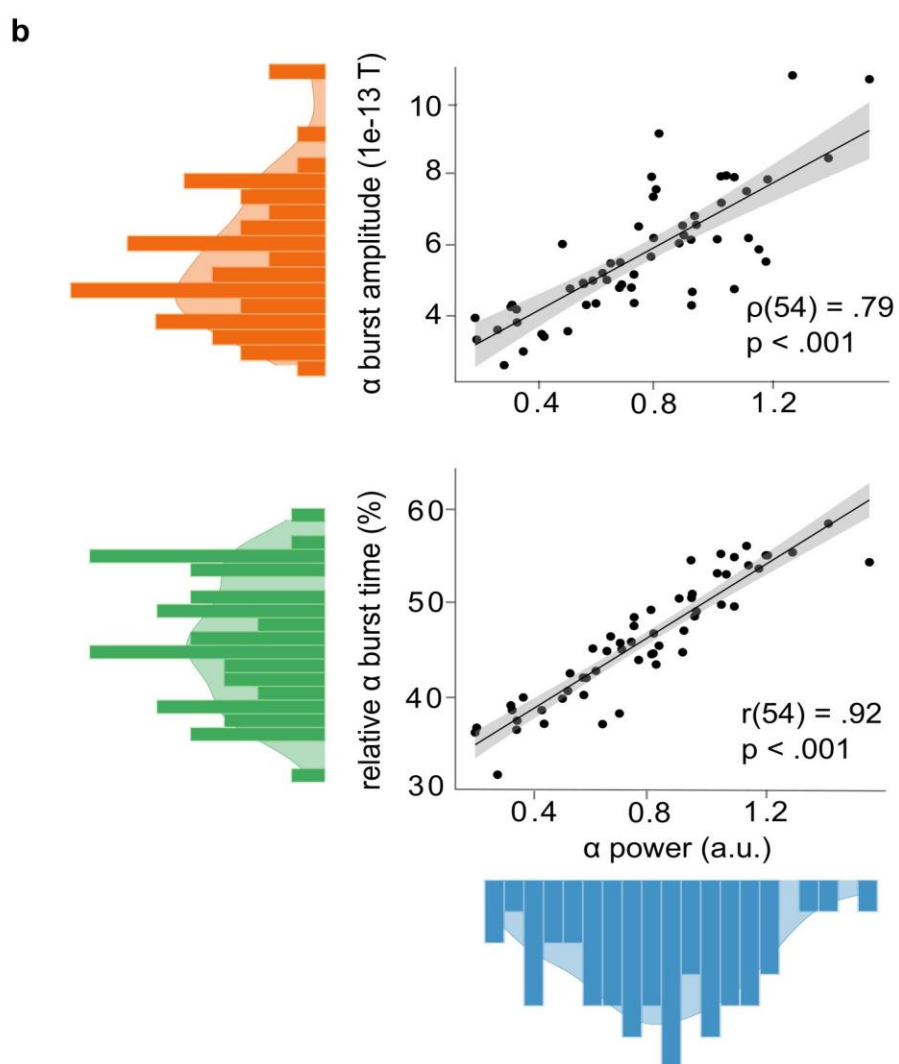
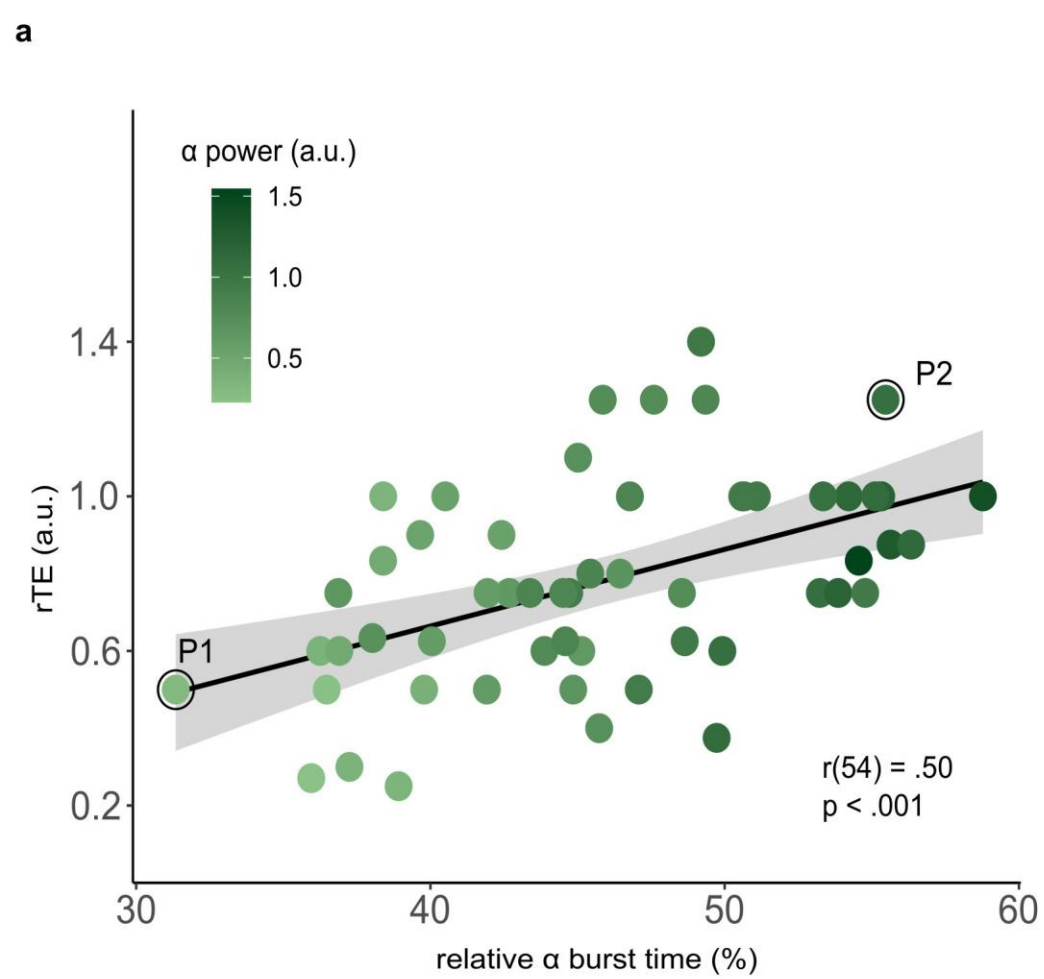
776 **Figure 1-1. α burstiness in gradiometers.** The same analysis performed in Fig. 2a was replicated with
777 gradiometers. The spontaneous α localizer resulted in 71 gradiometers used for the α cycle-by-cycle
778 analysis. Each dot represents an individual participant. The black line is the regression line and the grey
779 shading is 95% CI. A significant positive correlation between α power ($M = 0.76 \pm 0.28$ a.u.) and rTE
780 was observed. The correlation between rTE and relative burst time ($M = 45 \pm 6\%$) was also significant.

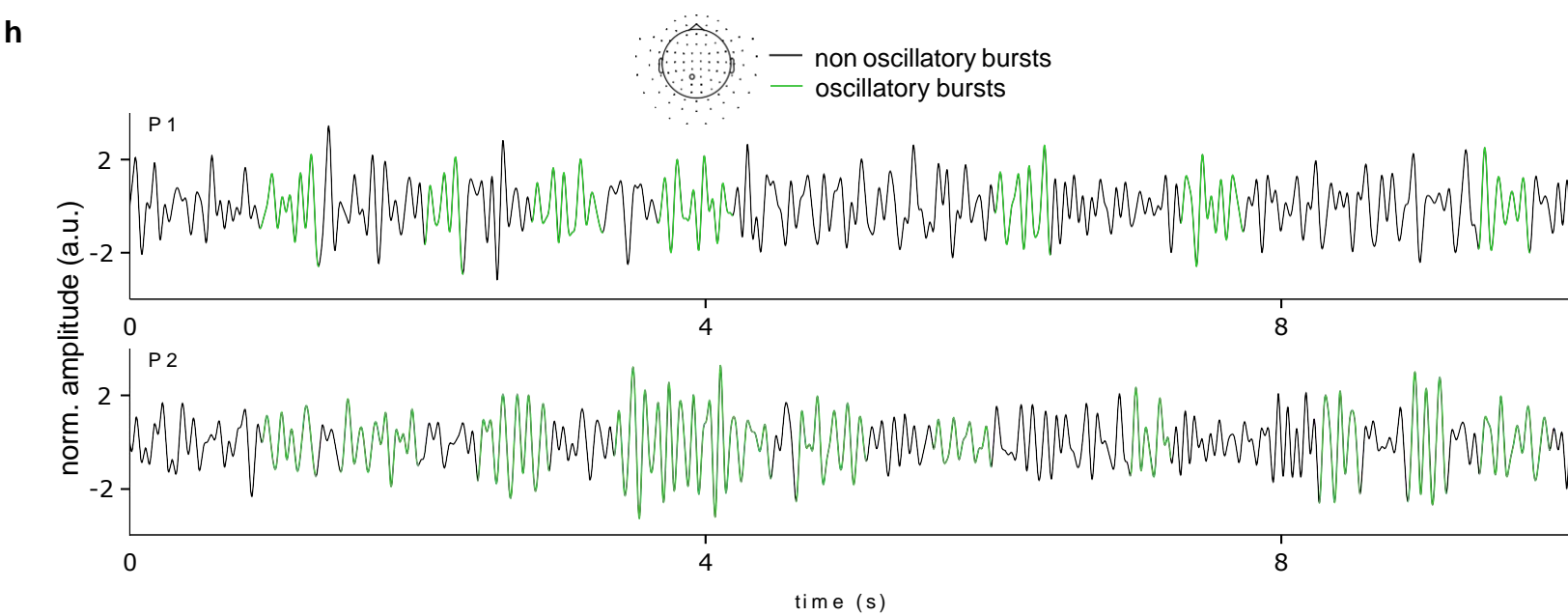
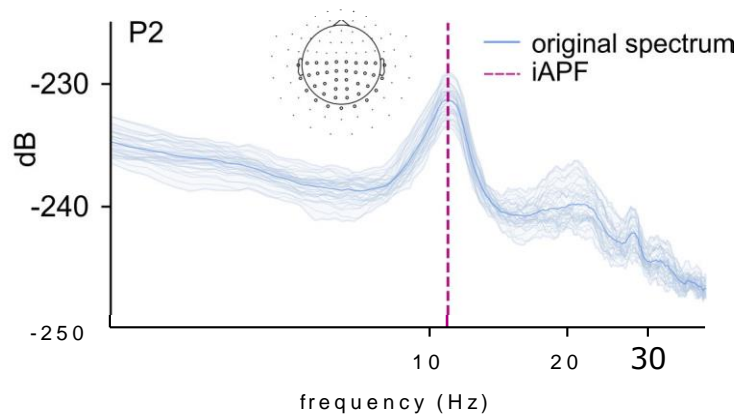
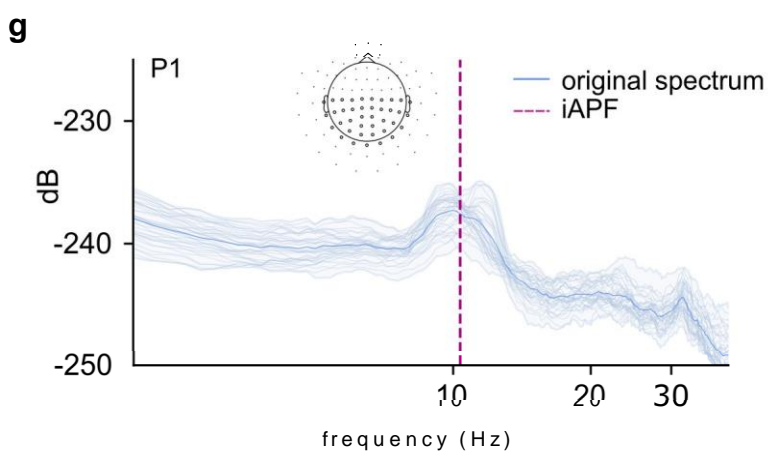
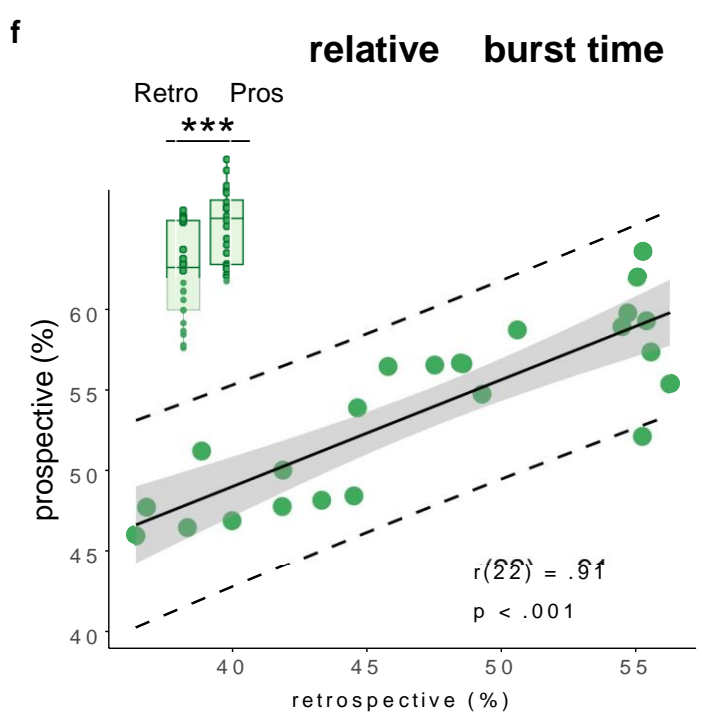
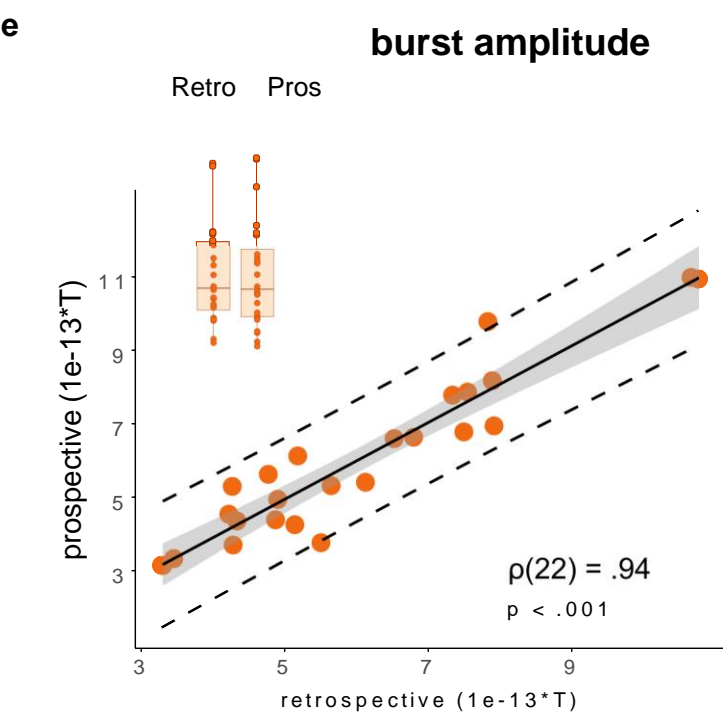
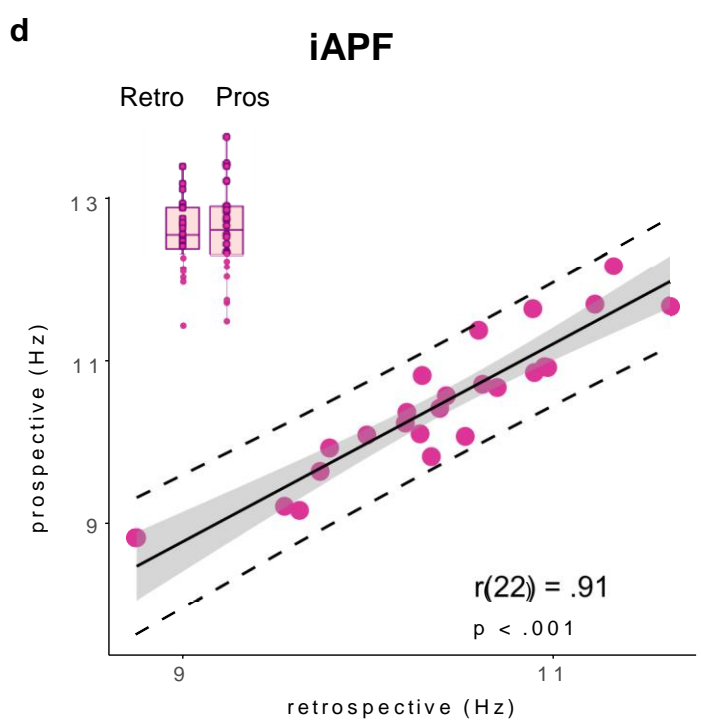
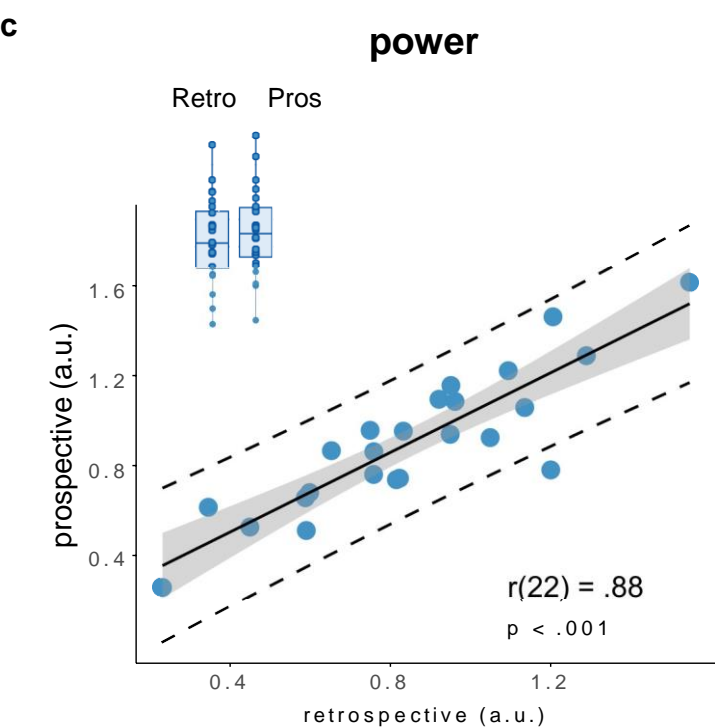
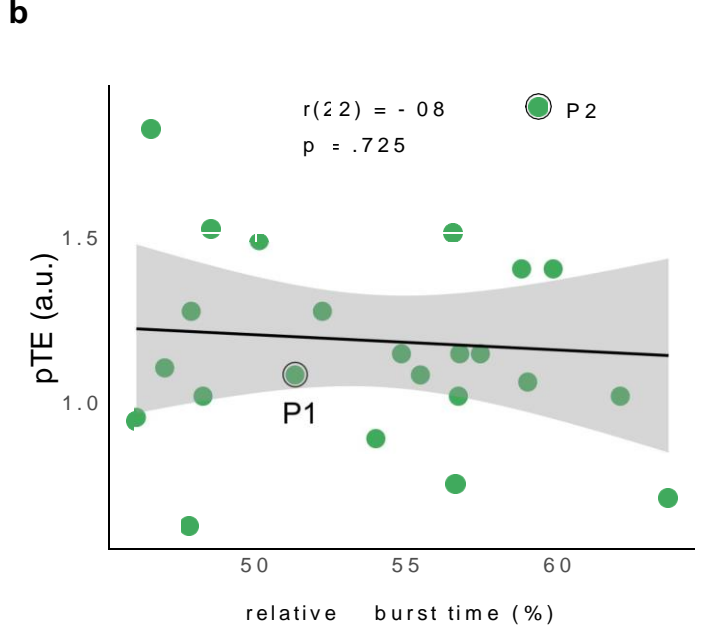
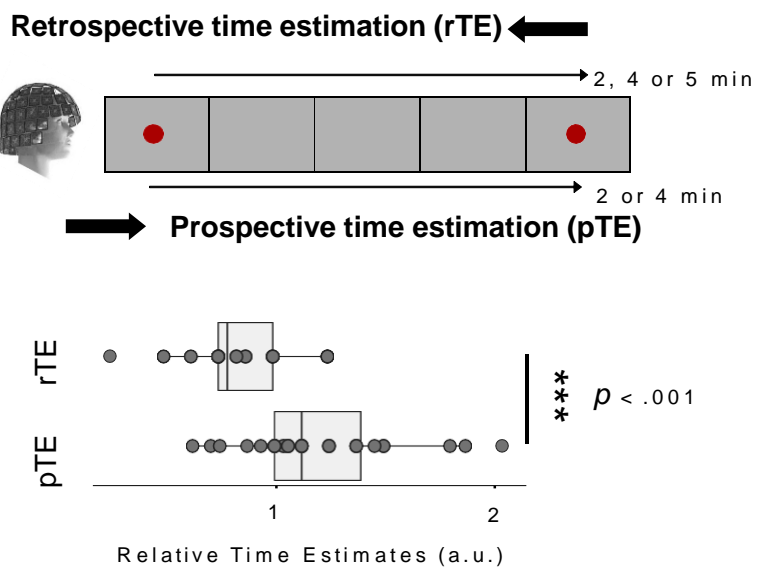
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782 **Figure 1-2. Cortical generators of α .** **a.** The grand-average source estimates of α activity collected in the
783 main retrospective task was computed across participants ($N = 50$; 5 out of 56 participants did not have
784 aMRI). **b.** The same analysis performed for the prospective task data ($N = 22$; 2 out of 24 participants did
785 not have an aMRI).

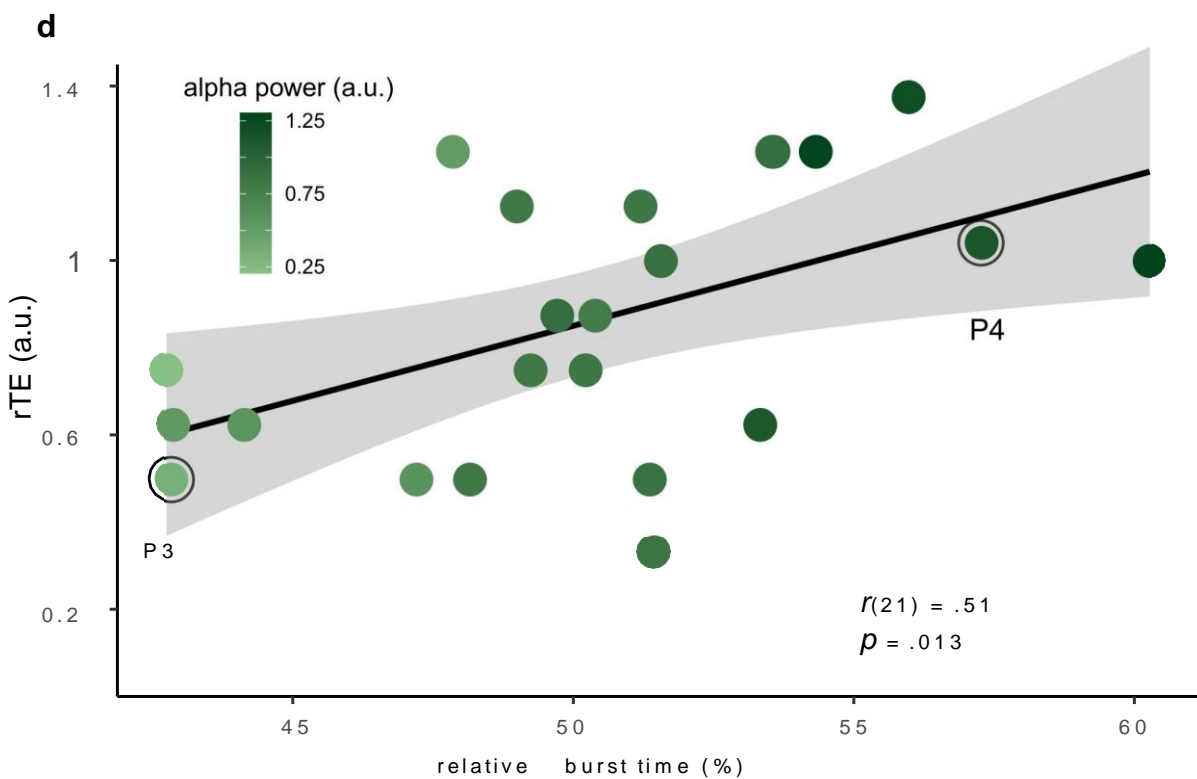
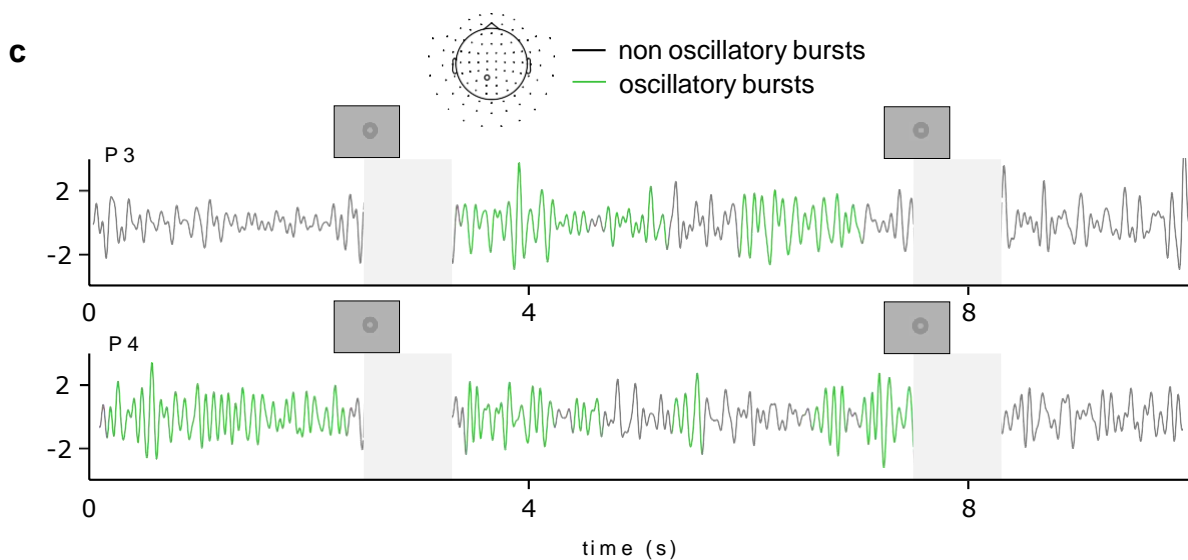
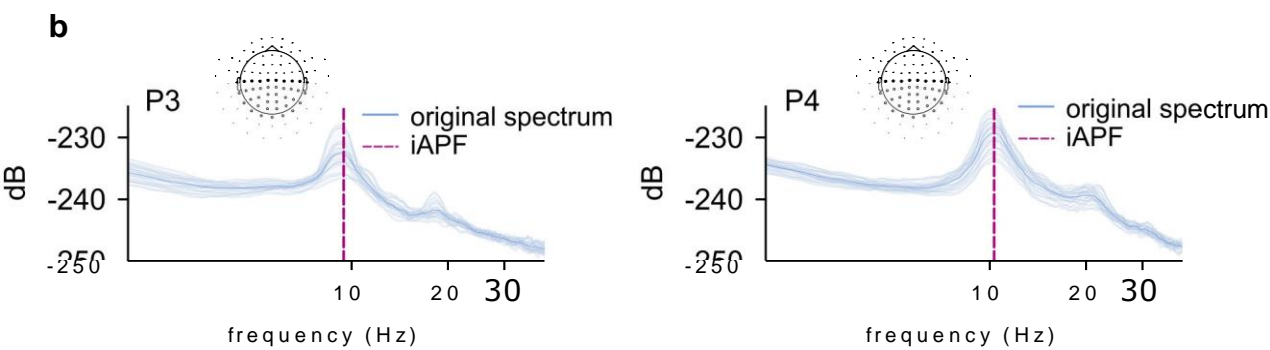
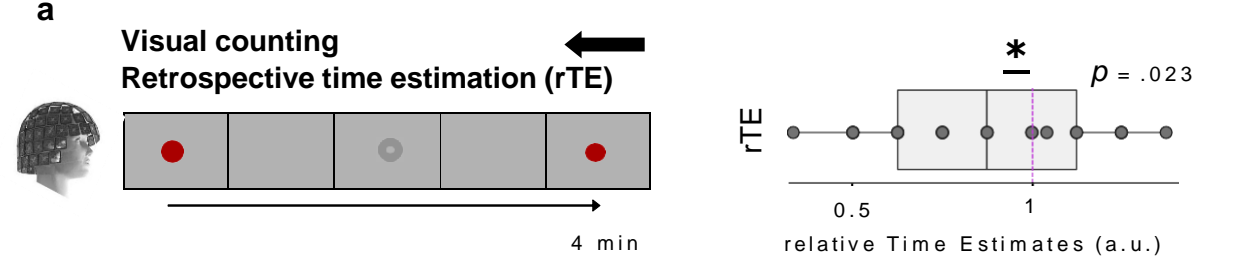
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787 **Figure 1-3. No relationship between an individual's α peak frequency (iAPF) and retrospective**
788 **duration estimation (rTE).** Each dot represents an individual. The black line is the regression line and
789 the grey shading is 95% CI. **a.** Magnetometers: no significant correlations were found between rTE and
790 iAPF. The mean iAPF was 10.5 Hz (± 0.78 Hz). **b.** Gradiometers: no correlations between iAPF and
791 rTE. Black lines are regression lines and shaded areas are 95% CI.

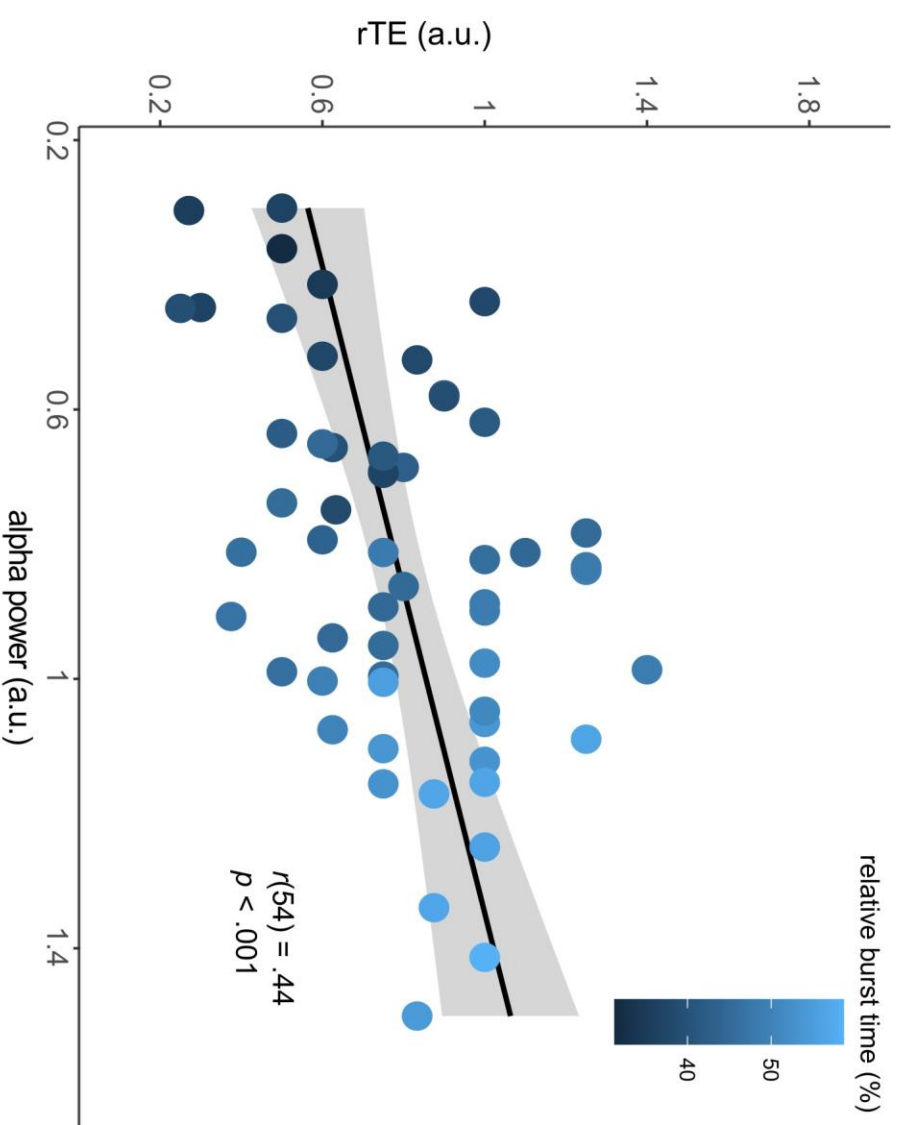
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793 **Figure 2-1. Stability of spontaneous α dynamics during quiet wakefulness.** To test whether the
794 properties of α dynamics showed a continuous trend in the course of the MEG recordings, we computed
795 the α power, the iAPF, the α burst amplitude and the relative α burst time in moving windows of 30 s over
796 the first 240 s of the quiet wakefulness recordings ($n = 41$; 4 min and 5 min conditions). Each dot
797 represents an individual participant. Non-parametric repeated measures Friedman test (non-normal
798 distribution) were performed using time windows (8) as main factor. One boxplot is a time window. **a.** A
799 main effect of windows was found on α power ($\chi^2(7, 40) = 67.3, p < .001$). A pairwise Wilcoxon signed
800 rank test showed that α power showed initially less amplitude than in the rest of the recording ($*p < .001$)
801 with α power reaching a plateau within 60s ($p = 1$). **b.** iAPF was stable throughout and did not change
802 over time ($\chi^2(7, 40) = 7, p > .05$). α burst amplitude (**c**) and relative burst time (**d**) were initially
803 significantly lower than in the rest of the recordings (α burst amplitude: $\chi^2(7, 40) = 61.7, * p < .001$;
804 relative α burst: $\chi^2(7, 40) = 53.7, * p < .001$).





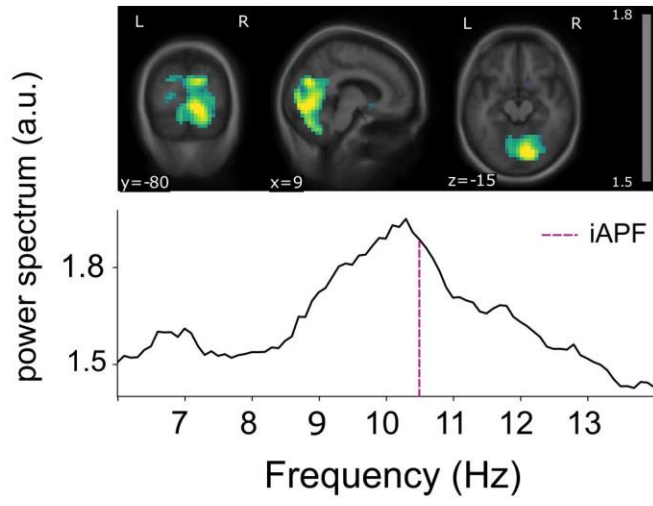




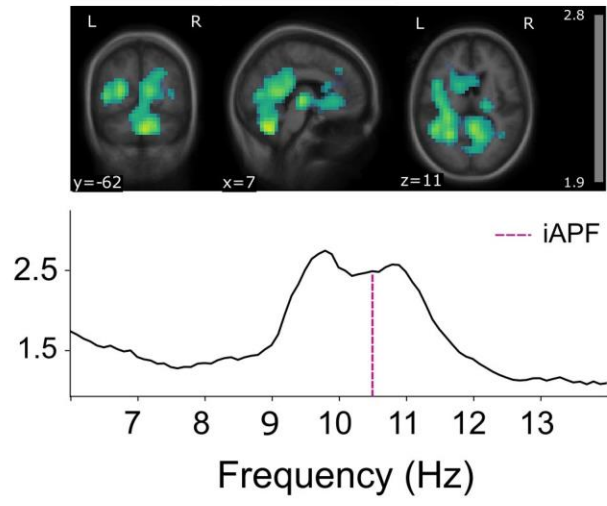


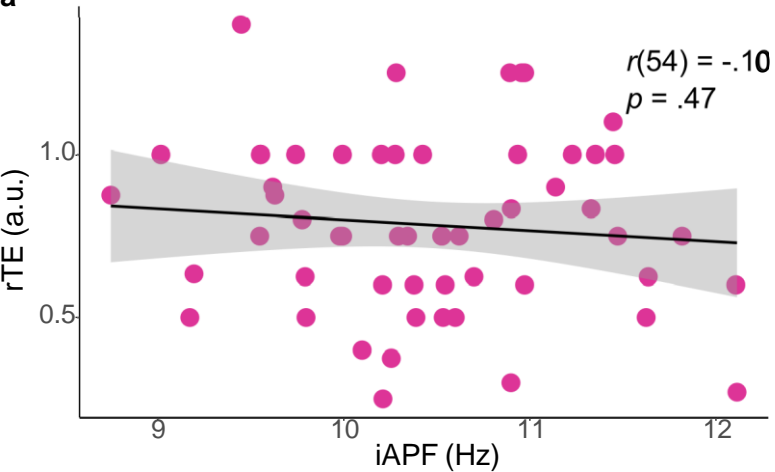
a

retrospective

**b**

prospective



a**b**