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Alpha/beta power compresses time in sub-second temporal judgments

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ABSTRACT

While the perception of time plays a crucial role in our day-to-day functioning, the underlying neural mechanism of time processing on short time scales (~1s) remains to be elucidated. Recently, the power of beta oscillations (~20 Hz) has been suggested to play an important role in temporal processing. However, the paradigms supporting this view have often had confounds of working memory, as well as motor preparation. In the current EEG study, we set out to investigate if power of oscillatory activity would be involved in time perception without an explicit working memory component or confound of a motor response. Participants indicated through a button press whether the time between a tone and a visual stimulus was 1 or 1.5s. Critically, we focused on the differences in oscillatory activity in the alpha (~10 Hz) and beta (~20 Hz) ranges preceding correct versus incorrect temporal judgments. Behaviourally, we found participants made more errors on the long (1.5s) than on the short (1s) interval. In addition, we found that participants were fastest to correctly respond to a long interval. The onset of the tone induced a suppression of alpha and beta activity over occipital and parietal electrodes. In the long estimation intervals, this suppression was greater for correct than incorrect estimations. Interestingly, alpha and beta suppression allowed us to predict whether participants would judge the long interval correctly. For the short interval trials we did not find a significant difference in alpha or beta band activity for the correct and incorrect judgments. Taken together, our behavioural and EEG results suggest a multifaceted role of alpha and beta activity in the temporal estimation of sub- and supra-second intervals, where power increases seem to lead to temporal compression. Higher alpha and beta power resulted in shorter temporal judgments for sub-second intervals.

Highlights

- Temporal judgments without motor confounds were studied with EEG.
- Alpha/beta activity differences for correct and incorrect temporal judgments.
- Sub-second intervals were judged as short when alpha/beta power was higher.

Keywords

Alpha, beta, time estimation, temporal judgement, EEG

42   **1. INTRODUCTION**

43   Time perception and human experience are tightly bound and play an important role in our

44   everyday life (e.g. when playing whack-a-mole at a fun fair). Understanding how we perceive

45   the passage of time has been an endeavour in psychology and neuroscience for over half a

46   century (Matthews & Meck, 2016; James, 1890). And although it is well known that the

47   human brain has a dedicated brain region for circadian rhythms (Turek, 1985), the neural

48   underpinnings of time perception on shorter time scales (~1s) remain to be elucidated

49   (Muller & Nobre, 2014).

50   Recent studies (Bartolo & Merchant, 2014; Kulashekhar et al., 2016; Kononowicz & van Rijn,

51   2015) suggest that beta oscillations (~15-25 Hz) play an important role in temporal

52   processing. Kononowicz & van Rijn (2015) found that in a self-paced key-press task, trial-to-

53   trial beta power over a central-motor electrode site positively correlated with the length of

54   produced durations. Crucially, this correlation was present for the pre-interval period (before

55   the first button press) and during the interval period (between the first and second button

56   press). However, given changes of the beta rhythm locked to the onset of motor responses

57   (Pfurtscheller & Lopes da Silva, 1999), it remains to be elucidated if beta oscillations, outside

58   the scope of motor production, are involved in temporal judgments.

59

60   Kulashekhar et al. (2016) found that beta band power increased while storing and retrieving

61   temporal but not colour information. This important finding suggests that beta oscillations are

62   indeed involved in temporal judgments, specifically in the memory encoding and retrieval of

63   temporal information. However, it remains unclear if beta oscillations were directly involved

64   in the perception of time, because temporal information was contrasted with colour

65   information.

66

67   In the current study, we set out to investigate how the modulations of oscillatory activity in

68   the alpha (8-12 Hz) and beta range would be involved in a temporal perception task without

69   an explicit working memory component or confound of a motor response. In addition to

70   activity in the beta range, we focused on alpha activity (~10 Hz) given its previously

71   established role in working memory (Lakatos et al., 2008; Haegens et al., 2010; Wilsch et al.,

72   2014), cross-modal attention (Van Diepen and Mazaheri, 2017, Foxe et al., 1998), and

73   perception (Van Dijk et al., 2008). We utilized a simple forced-choice temporal estimation

74   task where participants indicated by button press whether they judged the time between a

75   tone and a visual stimulus as 1 or 1.5s. We focused on the differences in EEG activity

76   between correct and incorrect temporal judgments in the interval between the tone and

77   visual stimulus. In addition to looking at the condition differences in alpha and beta power

78   between correct and incorrect judgments, we also examined if on a trial-by-trial basis power

79   modulations in those frequencies predicted accuracy of temporal judgments.

80

81

82   **2. MATERIALS AND METHODS**

83

84   *2.1 Participants*

85

86   Twenty-three healthy, young adults (right and left handed) participated in this study. Data

87   from three participants was excluded (one participant presented severe muscle artefacts

88   (>25% of trials), one participant did not make any errors in the short interval, one participant

89   made only 5 errors in the long interval). Twenty datasets were used for further analyses (13

90   females, mean age: 27 years, range: 19-41 years, 3 left handed). Participants had normal or

91   corrected-to-normal vision and hearing and they had no known history of neurological

92   disorders. In concordance with university guidelines, participants were paid £6 or 1

93   participation credit per hour. Participants gave written informed consent before data

94   collection. Ethical approval was provided by the Ethics Committee of the University of

95   Birmingham.

96

97   *2.2 Paradigm*

98

99   We utilized a novel two-forced-choice temporal judgement paradigm where the participant's

100   task was to estimate whether the time between an auditory stimulus and a visual stimulus

101   was short (1s) or long (1.5s), via a button press (Fig. 1). The paradigm was programmed in

102   Matlab (Natick, MA) using Psychophysics Toolbox extension (Brainard, 1997; Pelli, 1997;

103   Kleiner et al, 2007; psychtoolbox.org). The auditory stimulus was a pure tone of 1000 Hz,

104   which was administered through headphones (Sennheiser, HD 280 PRO) and lasted for

105   50ms (including a 5ms rise and fall shaped by a Blackman window). The tone signified the

106   start of the interval, which was followed by a visual stimulus that indicated the end of the

107   interval. The visual stimulus was a Gabor patch (angle 5° clockwise, contrast 80%, spatial

108   frequency 10 Hz, phase 0°), which lasted for 50ms. Short and long intervals were randomly
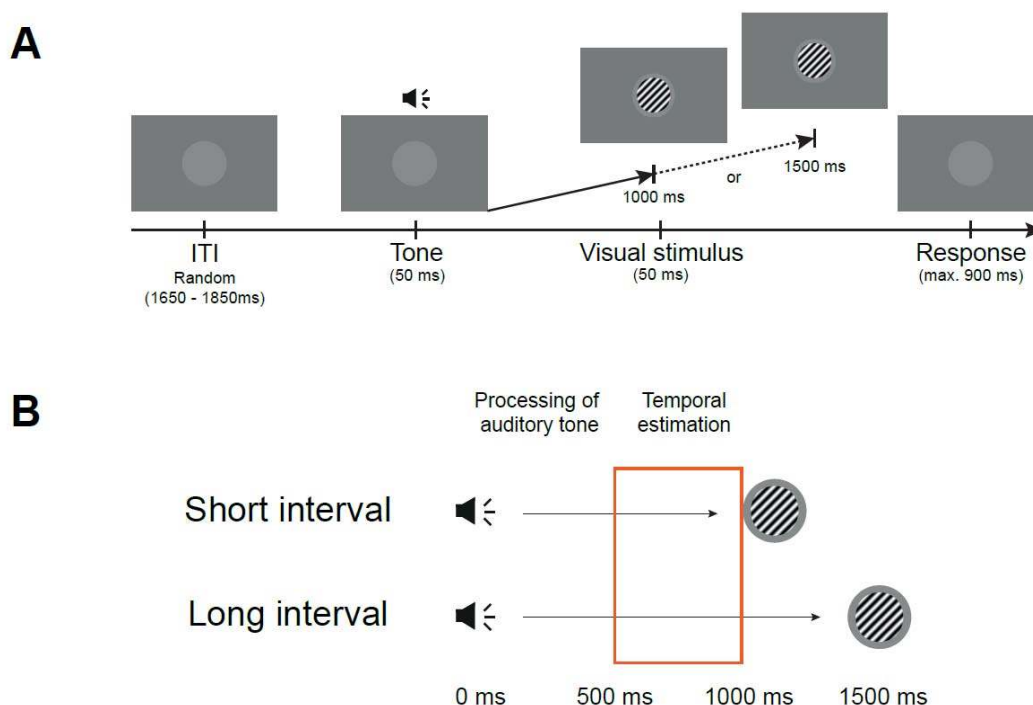
109   interspersed.

110

111

112

113   **Figure 1. Experimental paradigm and predictions.** Participants performed a two-forced-choice task estimating

114   the time interval between the tone and the visual stimulus (A). Trials were initiated with the presentation of a 1000

115   Hz pure tone for 50 ms. The tone was followed by a Gabor patch, which lasted for 50ms, 1 or 1.5s after the tone

116   was presented. Participants judged whether the interval between the tone and the visual stimulus was short (1s)

117   or long (1.5s) by pressing a button. Participants had 900ms to respond. After the response (or 900ms) a new trial

118   was initiated. A light grey placeholder was always on the screen to minimize eye movements. ITI = inter-trial

119   interval. Our time window of interest was before the short interval was over (1000ms) and after processing of the

120   auditory tone (~500ms; B). We hypothesized that differences between correct and incorrect trials would be

121   caused by differences in time estimation if the difference lay in the time window indicated by the orange box.

122

123

124   After the visual stimulus participants responded with a button press. If participants did not

125   respond within 900ms, a screen was displayed that read "Too slow! Please respond faster."

126   Participants were pushed to respond fast to enhance the likelihood that they would make

127   errors. Participants used the index (left button) and middle (right button) finger of their right

128   hand to respond. Response buttons were randomly counterbalanced across participants.

129   The dataset presented here contains data of 11 participants that pressed the left mouse

130   button for the long interval and 9 participants that pressed the right mouse button for the long

131   interval.

132

133 Participants were seated at a comfortable distance from the computer screen. The distance
134 was then measured and used to ensure a visual angle ~4° across all participants. To assure
135 participants kept their eyes on the screen a light grey placeholder was presented centrally on
136 the grey background (Fig. 1). The placeholder was 5% larger than the Gabor patch, so the
137 Gabor patch fell inside the placeholder.
138
139 Participants practiced for 3 blocks that consisted of 12 trials each. Participants received
140 feedback after each block. The EEG recording started by collecting resting state data with
141 eyes open and eyes closed for 30s each. This procedure was performed twice, randomly
142 starting with either eyes closed or eyes open data collection. The resting state EEG data
143 was not used for the purpose of this study. Following this, participants performed 16 blocks
144 of 60 trials, yielding a total of 960 trials per participant. Each block lasted ~3min and
145 participants were instructed to rest their eyes in between blocks. The refresh rate of the
146 screen was 60Hz and all timings of the experiment were set as multiples of this refresh rate.
147
148 *2.3 Behaviour*
149
150 Behavioural measures consisted of response times and error rates. Response times were
151 calculated from visual stimulus onset until response. Errors were calculated for each interval
152 condition separately by calculating the percentage of errors (i.e. judgment accuracy) relative
153 to the total number of trials in that condition. Statistical analyses were performed on
154 response times and errors, where the subject-specific averages were subjected to repeated-
155 measures ANOVA. For response time the factors were interval (short or long) and response
156 (correct or incorrect). For judgement accuracy (i.e. correct and incorrect judgments) the
157 factor was interval (short or long).
158
159 *2.4 EEG Data Acquisition*
160
161 EEG was acquired using the EEGO Sports system (ANT Neuro, Enschede, Netherlands)
162 and Waveguard caps housing 64 Ag/AgCl electrodes arranged in a 10/10 system layout
163 (including left and right mastoids, CPz as reference and AFz as ground). Impedances were
164 kept below 20kΩ, and the data was acquired using a sampling rate of 500Hz. EOG was
165 collected for horizontal eye movements, by placing bipolar electrodes on the outer canthi of
166 the left and right eye. ECG was collected for heart rate data, by placing one bipolar electrode
167 on the right chest, one bipolar electrode on the left abdomen and one bipolar electrode on
168 the left collar bone. This latter electrode acted as a ground electrode for the ECG signal.
169 Offline data analysis took place in Matlab with eeglab functions (version 13.1.1b; Delorme &

170   Makeig, 2004) and the FieldTrip software package (Oostenveld, Fries, Maris & Schoffelen,
171   2011).

172

173   *2.5 Preprocessing*

174

175   2.5.1 TFR analyses

176

177   Using EEGLAB, the data was epoched around -1000 to 3500 ms from tone onset.
178   Subsequently, a baseline from -100 to 0 ms was applied to the data to reduce DC offset.
179   Missed trials were discarded, as well as trials where the timing of the event triggers deviated
180   more than 2 ms of the intended timing. This last step was performed because timing was
181   crucial in this experiment and we wanted to exclude trials that deviated more due to
182   unforeseen slowness of the operating system of the stimulus computer. Based on visual
183   inspection trials were removed for the following reasons: muscle artefacts, noise (i.e.
184   electrode jumps or other electrode related noise), horizontal eye movements and blinks at
185   visual stimulus presentation. An average reference (excluding bipolar electrodes) was
186   applied to the cleaned data, and then CPz was reconstructed. Ocular artefacts were
187   removed in FieldTrip using independent component analysis (ICA, infomax algorithm)
188   incorporated as the default "runica" function. Prior to the ICA, a PCA (15 components) was
189   performed on the data, to speed up the ICA procedure.

190

191   2.5.2 Time Frequency Representation

192

193   Using the FieldTrip function 'ft_freqanalysis_mtmconv' time frequency representation (TFR)
194   of power was obtained for each trial by performing a fast fourier transform using a Hanning
195   taper in combination with a sliding time window. The time window was adapted to the
196   frequency of interest ($\Delta T = 3/f$). The frequency range of interest was from 2 to 40 Hz in steps
197   of 1 Hz. TFRs were calculated for the long and short interval and for correct and incorrect
198   responses separately, leading to 4 different subsets of trials. After we assessed that there
199   were no differences in baseline (i.e. pre-cue) oscillatory power for our frequency bands of
200   interest between correct and incorrect responses, data in each condition was normalized to
201   be the relative change in power according to the following formula,

202

$$\Delta p = (P_t - P_r) \; / \; P_r$$

203

204   where P_r was the mean power during the pre-cue period (700 – 200ms before tone onset)
205   and P_t was the power at each specific time point.

206   *2.6 Statistics*

207

208   2.6.1 TFR analyses

209

210   Our selection of frequency bands were loosely based on previous literature (Palva & Palva,

211   2007; Weisz et al., 2011; Zumer et al., 2014). Our statistical comparisons were made for the

212   alpha (8-14 Hz) and beta (15-25 Hz) band, between correct and incorrect responses for the

213   short and long interval separately. We did not directly compare the short and long intervals,

214   due to the fact that the amount of spectral leakage from the response evoked by the auditory

215   tones was different over short and long intervals.

216

217   The differences in oscillatory power between conditions were statistically assessed by

218   means of the cluster level (channels and time-points) randomization approach (Maris and

219   Oostenveld, 2007). Here, the power of the frequencies of interest in each channel and time

220   point within the time intervals of interest, were clustered according to exceeding a threshold

221   of $p < .05$ obtained from a two tailed dependent samples t-test. The time interval of interest

222   was 500-1000ms after tone onset for both frequency bands (Fig. 1B). Note that this was well

223   after processing of the auditory cue or start point of the interval and when the short time

224   interval ended. Next, the Monte Carlo p-values of each cluster were obtained by randomly

225   swapping the condition labels within participants 2500 times. A difference between

226   conditions was deemed significant if the cluster p-value was smaller than .025 (two-sided

227   test).

228

229   2.6.2 Power differences predictive of temporal judgments accuracy

230

231   Finally, we asked whether power differences in the clusters we identified were predictive of

232   time-estimation accuracy. To assess this, at the first level we fitted logistic regression

233   models (with the Matlab function 'glmfit') of alpha or beta power, averaged over the cluster

234   that showed the maximal difference between conditions, as a predictor of response accuracy

235   (short or long). To apply this model to ordinal data we used the logit link function. This model

236   yields a Beta weight for each participant. We then tested the significance of these Beta

237   weights across-participants with a permutation test. In this permutation test a random sign

238   was assigned to the observed Beta values, which allowed us to build a distribution for the

239   null hypothesis. We then checked whether our mean observed Beta value was as extreme

240   or more extreme than the outer 2.5% of the null distribution (two-sided test).

241

242   To visualize our effect, we approached our data in two ways. First, we plotted accuracy as a

243   function of binned z-scored alpha and beta power in 5 equal-sized bins within a participant.

244   We used z-scored power because this reduced the variability between participants. The z-

245   scored power was calculated according to the following function:

246

$$z = \frac{power_t - \mu(power)}{std(power)}$$

247

248   where z is the z-scored power, $power_t$ is the power for the trial on which the z-scored power

249   is calculated, $\mu(power)$ is the average power of all trials and $std(power)$ is the standard

250   deviation of all trials. Second, we plotted the logistic regression lines for normalized power

251   within participants. Normalized power was obtained as following:

252

$$normalized\ power_{correct} = \frac{(\mu(power_{correct}) - \min(power_{both})}{(\max(power_{both}) - \min(power_{both}))}$$

253

254   where normalized power$_{correct}$ represents the normalized power for each trial for correct trials.

255   Power$_{both}$ refers to power of both correct and incorrect responses. This approach yielded

256   normalized power values between 0 and 1, which ensured an equal length for each of the

257   regression lines. Please note that the regression line is the same for normalized or

258   unnormalized power. Moreover, the statistics explained above were only applied to the Beta

259   values that were obtained from logistic regression with baseline corrected power data.

260

261   **3. RESULTS**

262

263   *3.1 Behavioural*

264

265   3.1.1. Participants respond fastest on long correct trials

266

267   We first investigated if there were response time differences between correct and incorrect

268   responses on the short and long interval. In terms of main effects, we found a significant

269   effect of response ($F(1,19) = 49.882$, $p < .0001$, $\eta_p^2 = .724$), with responses being fastest for

270   correct responses (384.2 vs. 456.9ms). In addition we found a significant effect of interval

271   and interval length ($F(1,19) = 138.477$, $p < .0001$, $\eta_p^2 = .879$), with response time being

272   fastest for longer (i.e. 1.5s) versus shorter (i.e. 1.0s) temporal judgments (395.9 vs.

273   447.2ms).

274

275   We found that participants were fastest to respond in correctly perceived long intervals, with

276   a significant interaction effect of response × interval length (Fig. 2A; $F(1,19) = 33.394$, $p <$

277   .0001, $\eta_p^2 = .637$). Post-hoc analyses revealed for the longer temporal judgments

278   individuals were significantly faster on correct responses (329.0 ± 47.7ms, mean ± standard

279   deviation) than incorrect responses (458.8 ± 66.9ms). However, on the short interval we

280   observed no significant difference in response time between correct (439.3 ± 61.3ms) and

281   incorrect (454.9 ± 81.2ms) responses.

282

283   3.1.2. Participants made more errors during the long interval

284

285   We found that individuals made significantly more errors during the long interval trials than

286   during the short interval trials (long interval errors: 25.91 ± 13.23%; short interval errors: 9.68

287   ± 6.54%; $F(1,19) = 19.893$, $p \approx .0003$, $\eta_p^2 = .511$).

288

289
290
291   **Figure 2. Behavioural effects.** On the long interval (A; blue lines), individuals were significantly faster on correct

292   responses (329.0 ± 47.7ms, mean ± standard deviation) than incorrect responses (458.8 ± 66.9ms). On the short

293   interval (orange lines), no significant difference in response time between correct (439.3 ± 61.3ms) and incorrect

294   (454.9 ± 81.2ms) responses was found. Individual participant data is represented in opaque lines with open dots,

295   participant average data is depicted in the fat lines. Individuals made significantly more errors in the long interval

296   (B; 25.91 ± 13.23%) compared to the short interval (9.68 ± 6.54%). Error bars represent standard errors of the

297   mean.

298

299

300   *3.2 EEG results*

301

302   3.2.1. No difference in alpha/beta suppression in correct versus incorrect short interval (1s)

303   judgment trials

304

305   We set out to investigate if oscillatory activity between the tone and a visual target occurring

306   1s later could be predictive of states in which participants were more likely to over-estimate

307   the durations. The time-frequency representations of power between the auditory tone and

308   visual target interval collapsed across all electrodes can be seen in Figure 3A for correct

309   (left) and incorrect trials (right). For both correct and incorrect short interval judgments, the

310   onset of the cue induced a transient increase in theta activity, followed by a sustained power

311   decrease in alpha and beta bands starting ~500ms after tone onset. Shortly after the visual

312   cue was presented a more pronounced transient decrease in beta power can be seen

313   ~1300ms after tone onset, which roughly coincides with the button press (average RT for

314   correct and incorrect judgments was ~447ms).

315   To assess whether alpha and beta suppression were significantly different between correct

316   and incorrect judgments of the short interval, we used cluster based statistics correcting for

317   multiple comparisons. For the alpha band we found no significant difference in the time

318   window of interest (500-1000ms after tone onset). Subsequent examination of the alpha

319   activity within that time found the greatest difference in alpha modulation between correct

320   and incorrect trials to be from 750-800ms after tone onset, where correct trials had more

321   power than incorrect trials. However, this difference was not significant ($p > .06$). Figure 3C

322   (top) shows the average power difference between correct and incorrect trials averaged over

323   the entire time window of interest, irrespective of the cluster.

324

325   Similarly, for the beta band we found no significant difference in our time window of interest.

326   The difference between correct and incorrect trials was again strongest from 750-800ms

327   after tone onset, where correct trials had more power than incorrect trials ($p > .045$,

328   remember that our critical *p*-value is .025). Figure 3C (bottom) shows the average power

329   difference between correct and incorrect trials averaged over the entire time window of
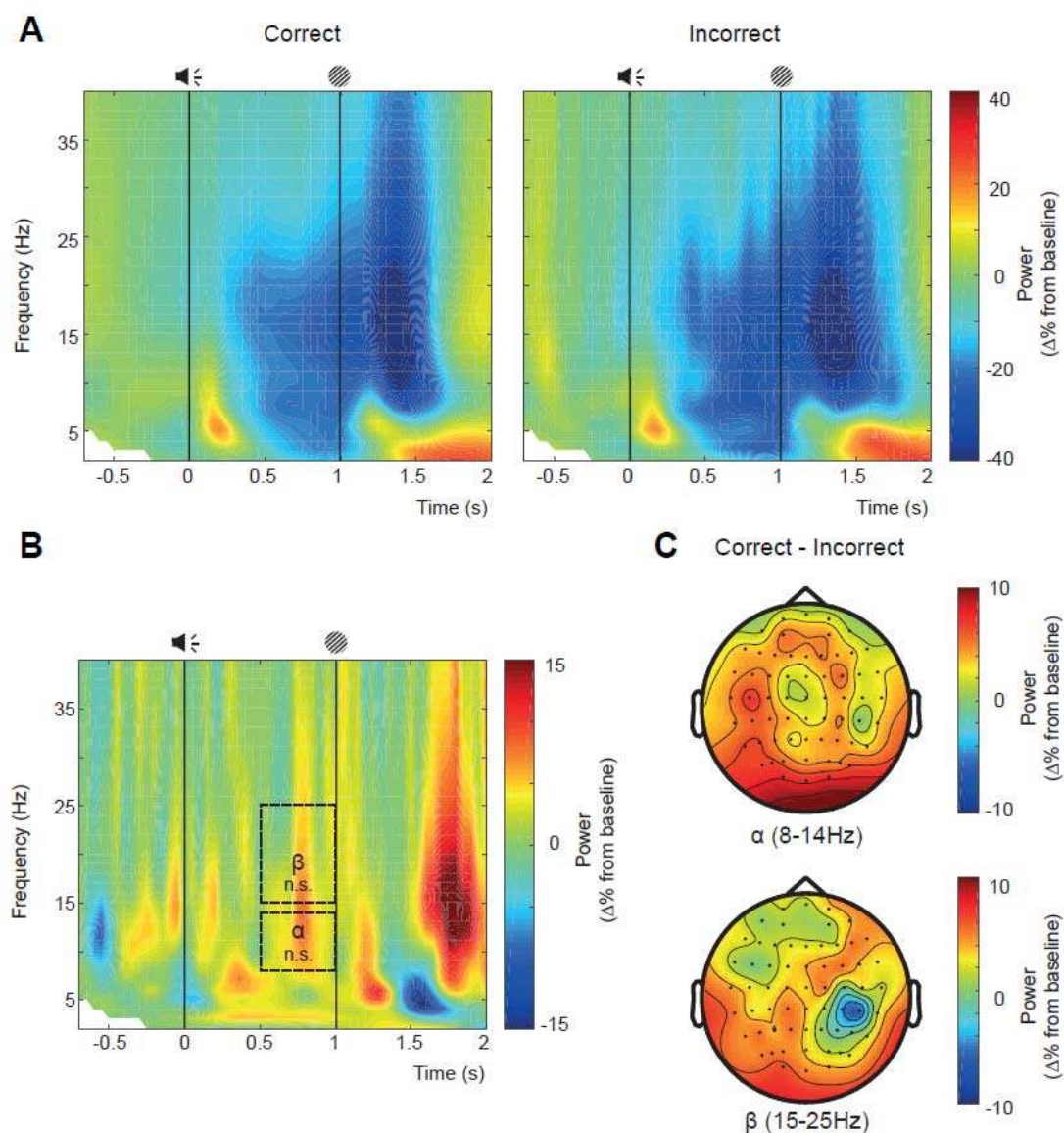
330   interest.

331

Figure 3. TFR for the short interval. The percentage change from baseline is plotted for the different frequency bands over time averaged across all electrodes, with a baseline interval from -700 to -200 ms, tone onset at t = 0 s followed by visual stimulus presentation at t = 1.0 s. Correctly perceived short intervals are visible on the left and trials incorrectly perceived as long are visible on the right (A). The difference plot shows more power for trials correctly perceived as short than trials incorrectly perceived as long (B). There were no significant differences observed in the alpha or beta band. The topography of the average activity over the time window of interest is plotted in C (correct – incorrect trials).

343 <u>3.2.2. Greater alpha/beta suppression in correct versus incorrect long interval (1.5s)</u>
344 <u>judgment trials</u>

345

346 As with the short-interval, the time-frequency representations of power between the auditory

347 cue and visual target interval collapsed across all electrodes can be seen in Figure 4A for

348 correct (left) and incorrect (right) trials. After the transient theta increase induced by the

349 onset of the auditory cues, we observed a sustained power decrease in alpha and beta

350 bands, from ~500ms to ~1700ms after tone onset. Moreover, a more pronounced transient

351 beta decrease was observed at ~1700-1900ms after tone onset. This beta decrease roughly

352 coincides with the button press (averaged RT for correct and incorrect trials was ~393ms).

353 To examine the sustained alpha and beta power decreases, we tested the interval of 500ms

354 after tone onset until visual stimulus onset of the short interval at 1000ms. However, we

355 should note here again that the onset of the visual stimulus was 1500ms in long interval

356 trials.

357

358 To assess whether alpha and beta suppression were significantly different between correct

359 and incorrect judgments of the short interval, we used cluster based statistics correcting for

360 multiple comparisons. For the alpha band we found a significant difference in our entire time

361 window of interest (500-1000ms after tone onset), where correct trials had less power than

362 incorrect trials ($p < .0024$). Figure 4C (top) shows the average power difference between

363 correct and incorrect trials averaged over the cluster where the difference was most

364 pronounced (outlined in Fig. 4B). The black dots with white edges represent electrodes that

365 were part of the cluster at any one time point from 500-1000ms.

366

367 Similarly, for the beta band we found a significant difference power between correct and

368 incorrect judgments in our time window of interest. The difference between correct and

369 incorrect trials was strongest from 600-1000ms after tone onset, where correct trials had less

370 power than incorrect trials ($p \approx .0004$). Figure 4C (bottom) shows the average power

371 difference between correct and incorrect trials averaged over the cluster where the

372 difference was most pronounced (outlined in Fig. 4B). The black dots with white edges

373 represent electrodes that were part of the cluster at any one time point from 600-1000ms.
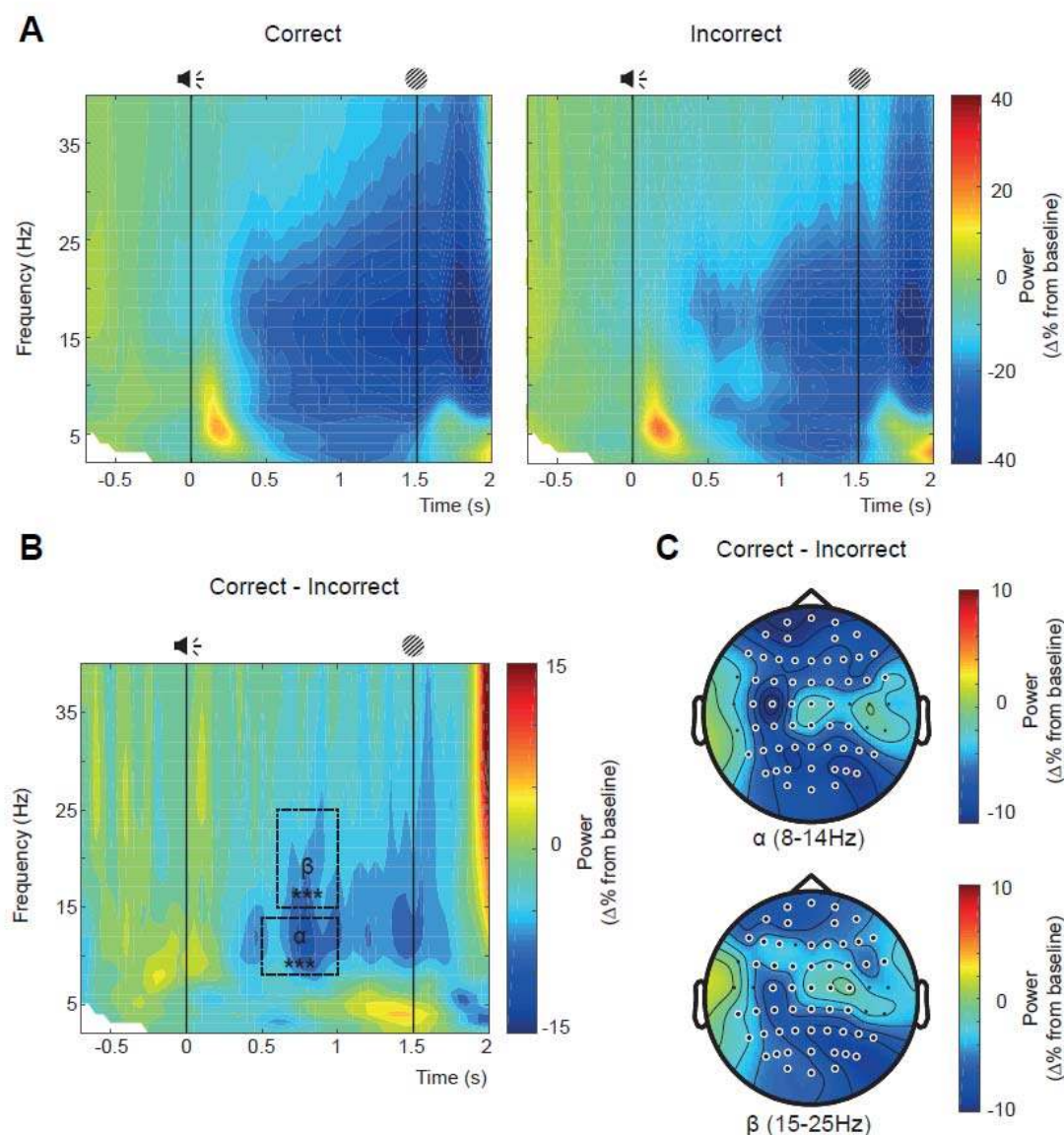
374

375

Figure 4. TFR and topographical distribution for the long interval. Same as in Fig. 3A but now with visual stimulus presentation at t = 1.5 s. The difference between correct (left in A) and incorrect (right in A) trial types is visualized in B, where power was lower for correct trials. Significant differences between correct and incorrect responses were observed in the alpha and beta bands. The topographical plots show correct-incorrect responses (C). Black circles with white edges represent electrodes showing significant modulation at any one time point, corrected for multiple comparisons using cluster randomization routine (Maris and Oostenveld, 2007).

3.3 Effect size

Finally, we calculated the effect size of our smallest TFR effect to ease future, direct replications of our reported effects. Please note that partial Eta squared was reported as effect size for our behavioural findings. To assess the effect size of our result, we used the

389   alpha cluster depicted in Figure 4C and took the difference between the averaged power

390   over trials for correct and incorrect responses to the long interval trials. The mean difference

391   of these power values was -7.02% with a standard deviation of 2.18%, which leads to a

392   Cohen's $d ≈ 3.22$. To replicate this finding a follow-up study, with 80% power and $α = .05$,

393   would need 4 participants.

394

395   *3.4 Response to auditory cue not different between correct and incorrect temporal*

396   *judgments*

397

398   Previous research suggested that expectation could allocate resources to a task-relevant

399   region (e.g. visual system) at the expense of processing in the task-irrelevant regions

400   (Cartwright-Finch and Lavie, 2007). Moreover, we wanted to make sure that any differences

401   we observed were not caused by differences in processing of the auditory cue. As such, we

402   investigated if the response to the auditory cue could be predictive of the accuracy of

403   temporal judgments. However, we did not find a significant difference in power between

404   correct and incorrect responses to the processing of the tone (50-300 ms after tone onset, 3-

405   6 Hz). There was no cluster for the long interval. For the short interval a non-significant

406   cluster was identified (p<.1), with the largest difference from 250-300ms after tone onset.

407

408   *3.5 Alpha and beta power predict temporal judgments in the long interval*

409

410   Here, we investigated whether a relationship between correctly identifying the temporal

411   durations and the power of alpha and beta activity could be observed on a trial-by-trial basis

412   To this end, we fitted logistic regressions to each individual participant's data and tested the

413   beta weights of these fits at the group-level against a null distribution obtained through a sign

414   permutation test (see Materials & Methods for more details).

415

416   A logistic regression model was fitted with a logit link function where alpha power for each

417   trial, averaged over the electrodes depicted in Figure 4C (top) and over time 500-1000ms

418   after tone onset, was used as a predictor of correct or incorrect responses. This approach

419   yielded a Beta value for each participant. To assess whether these Beta values were

420   significantly different from 0 (no predictive value) we used a permutation test. We found that

421   alpha power of the cluster we observed significantly predicted correct versus incorrect

422   responses ($p < .0001$). Similarly, we found that beta power for each trial, averaged over the

423   electrodes depicted in Figure 4C (bottom) and over time 600-1000ms after tone onset,

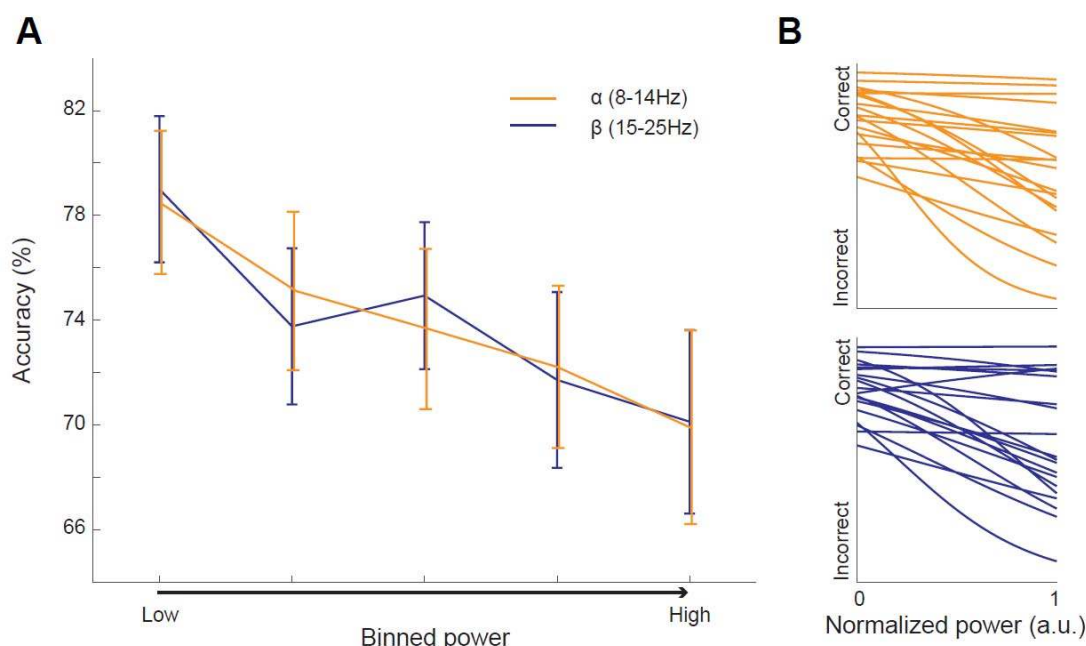424   predicted responses ($p = .0001$).

425

426

427

428

Figure 5. Accuracy as a function of power. Alpha and beta power from the clusters displayed in Figure 4C significantly predicted responses. This relationship is visualized here by plotting accuracy as a function of binned z-scored alpha and beta power, where each bin has the same amount of trials within a participant (A). As alpha and beta power increase, the accuracy decreases. Error bars represent standard error of the mean. The logistic regression lines for normalized power are shown in B (alpha on the top and beta on the bottom). Statistics reported in the text were performed on non-normalized power values to make sure that our normalization procedure did not drive the effect.

436

437   To further visualize this effect we binned z-scored alpha and beta power in 5 equal sized

438   bins for each participant (same number of trials in each bin within a participant) and plotted

439   accuracy as a function of binned power (Fig. 5A). As alpha/beta power increases

440   participants are more likely to judge a 1.5s interval as short. We also plotted the regression

441   lines of normalized power in Figure 5B. The power was normalized between 0 and 1 such

442   that the regression lines were of the same length. In the supplementary materials the

443   individual participant data can be viewed, with the logistic regression fits for each participant

444   (Supplementary Fig. 1). The Beta values of the regression lines in the supplementary figures

445   depicts the data on which statistics were performed.

446

447

448   **4. Discussion**

449   In the current EEG study, we set out to investigate how the power of ongoing oscillations

450   could be involved in time perception, controlling for the presence of an explicit working

451   memory component or confound of a motor response. Using a novel paradigm, we asked

452   our participants to judge the temporal interval between a tone and a visual stimulus as being

453   short (i.e 1s) or long (i.e. 1.5s). Our analyses focused on the activity preceding correct

454   versus incorrect temporal judgments. For both correct and incorrect short interval judgments,

455   we observed that the onset of the cue induced a transient increase in theta activity, followed

456   by a sustained power decrease in alpha and beta bands starting ~500ms after tone onset

457   and continuing till well after the visual stimulus. While we did not find any significant

458   differences in alpha or beta power modulation in correct versus incorrectly judged short

459   intervals, we did so for the long-interval judgments. Specifically, correct judgments of the

460   long interval had significantly greater alpha and beta suppression than incorrect judgments.

461   On a trial-by-trial basis we found that the more alpha/beta power increased in the 0.5-1s

462   window after cue onset, the more likely the participants were to judge a 1.5s interval as

463   short.

464

465   Behaviourally, we did not find any significant difference between correct and incorrect

466   responses for the short interval. In contrast, for the long interval, individuals were

467   significantly faster on correct responses than incorrect responses. Moreover, participants

468   made more errors when estimating long duration trials (1.5s) than when estimating short

469   duration trials (1s). This is in line with Webber's law, which predicts that it becomes

470   increasingly more difficult to estimate time as more time has passed by. In addition, we

471   found that individuals responded faster on correctly observed long intervals. This may

472   suggest that participants have a template of 1s in mind and when this time interval has

473   passed they expect the upcoming visual stimulus at 1.5s allowing the speeded response.

474

475   Taken together these behavioural findings may indicate that two different mechanisms

476   operate for short and long intervals. A differentiation between sub- and supra-second

477   intervals would be in line with previous literature (Lewis & Miall, 2003; Matell & Meck, 2004),

478   although it is disputable whether a 1s interval would be classified as a sub-second interval.

479   Alternatively, another explanation for these behavioural differences might be that the same

480   mechanism underlies both intervals, but that this mechanism does not get enough time to

481   unfold in the short interval. However, this alternative explanation cannot account for our

482   finding that individuals make more errors in the long.

483

484   Our EEG data showed no significant difference in power between correct and incorrect

485   judgments of short interval trials. For the long interval trials, we found a significant difference

486   between correct and incorrect responses in the alpha and beta band. Moreover, the cluster

487   that exhibited the largest difference between these trial types allowed us to predict whether

488   participants judged a trial as short or long. Interestingly, we were able to predict the

489   response before the short interval time window closed (<1000ms).

490

491   It remains to be elucidated why we did not find an effect of alpha/beta power for correct and

492   incorrect judgments of the short interval. One explanation might be that we simply did not

493   have enough incorrect judgments for these trial types, hampering our power to detect a

494   small effect. This explanation is in line with our insignificant results, where the clusters

495   showed more power for correct trials than incorrect trials, suggesting that power increases

496   condense temporal judgments and bias participants to judge an interval as short.

497   Alternatively, a different mechanism might operate for sub- and supra-second time interval

498   judgments. Future research should investigate this.

499

500   In accordance with Kononowicz & van Rijn (2015), we found that alpha/beta power

501   fluctuations might represent a neural signature that is used to track time. Kononowicz & van

502   Rijn (2015) showed that self-paced intervals that were longer than the target interval had

503   more beta power. In the current study, we showed that increased alpha/beta power leads to

504   underestimation of the time that has passed by. Taken together, this suggests that high

505   alpha/beta power leads to compression of the time that has passed by. From this framework

506   it would follow that crossing a certain threshold leads to experiencing a temporal window as

507   shorter. It will be exciting to see if these findings replicate and how the difference between

508   sub- and supra-second time intervals can be explained, but our findings capitalize on the

509   importance of oscillatory activity in time processing. In summary, in the current study we

510   found that modulations in alpha and beta power were predictive of temporal judgments.

511   Specifically, increased alpha/beta power between the cue-target interval biased participants

512   to report the long intervals as being short. We hypothesize that fluctuations in alpha/beta

513   power condense the subjective experience of time passing by.

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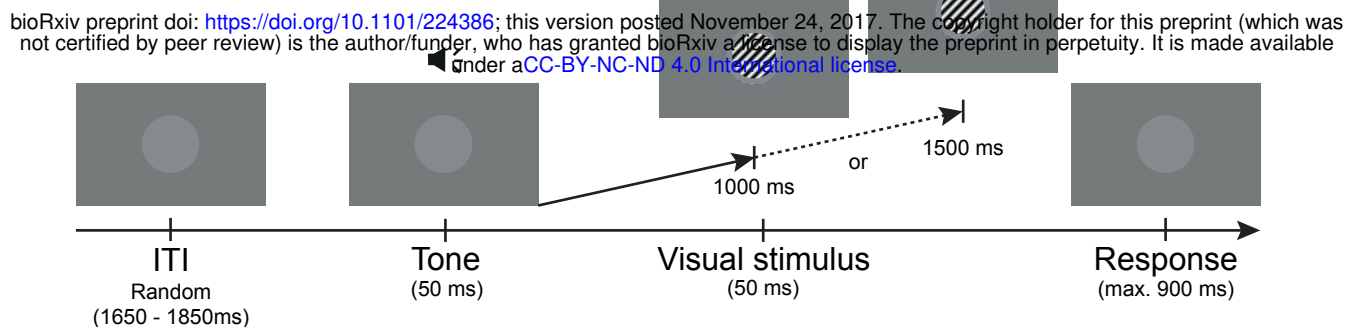621   1938–46.

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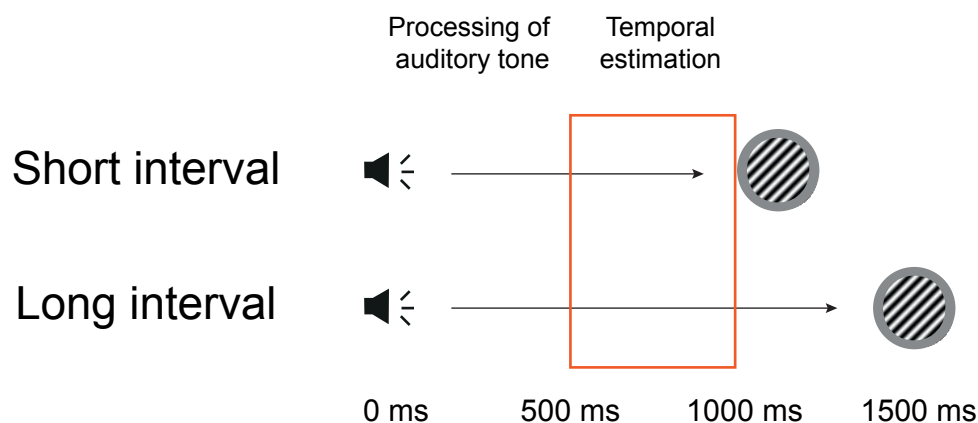625   Selective Cortex." *PLoS Biology* 12 (10): e1001965.

Figure 1. Experimental paradigm and predictions. Participants performed a two-forced-choice task estimating the time interval between the tone and the visual stimulus (A). Trials were initiated with the presentation of a 1000 Hz pure tone for 50 ms. The tone was followed by a Gabor patch, which lasted for 50ms, 1 or 1.5s after the tone was presented. Participants judged whether the interval between the tone and the visual stimulus was short (1s) or long (1.5s) by pressing a button. Participants had 900ms to respond. After the response (or 900ms) a new trial was initiated. A light grey placeholder was always on the screen to minimize eye movements. ITI = inter-trial interval. Our time window of interest was before the short interval was over (1000ms) and after processing of the auditory tone (~500ms; B). We hypothesized that differences between correct and incorrect trials would be caused by differences in time estimation if the difference lay in the time window indicated by the orange box.
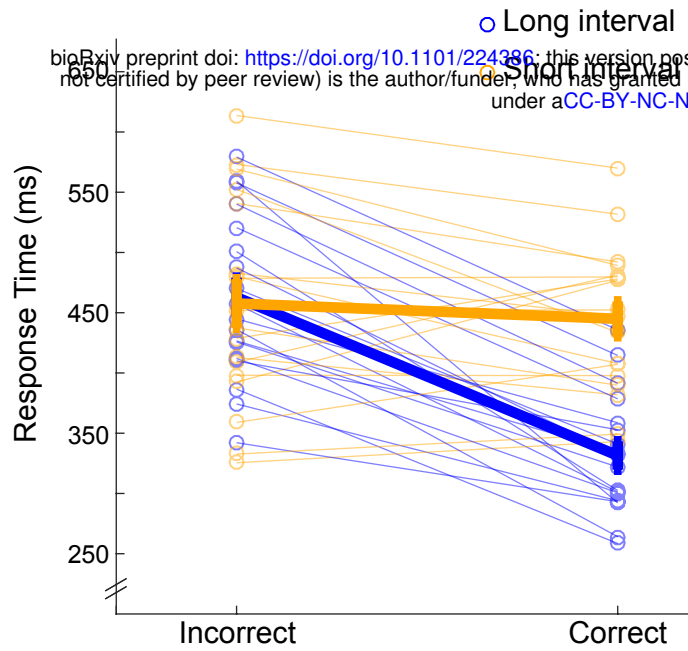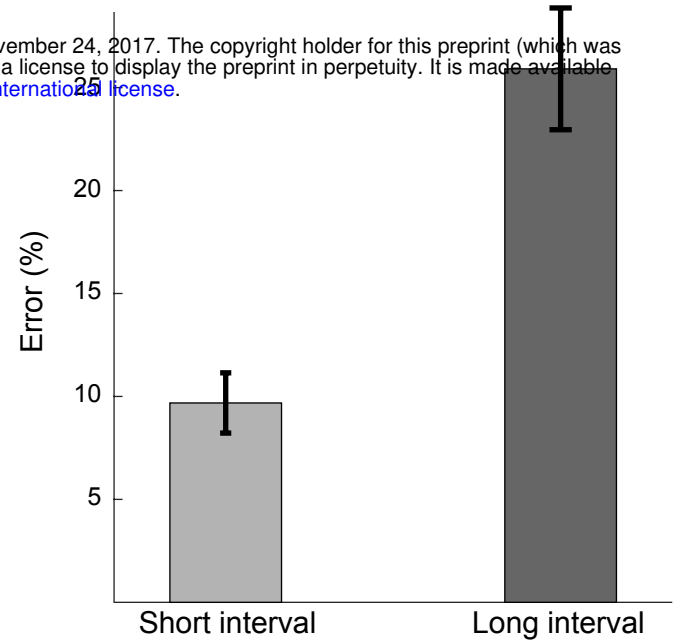
Figure 2. Behavioural effects. On the long interval (A; blue lines), individuals were significantly faster on correct responses (329.0 ± 47.7ms, mean ± standard deviation) than incorrect responses (458.8 ± 66.9ms). On the short interval (orange lines), no significant difference in response time between correct (439.3 ± 61.3ms) and incorrect (454.9 ± 81.2ms) responses was found. Individual participant data is represented in opaque lines with open dots, participant average data is depicted in the fat lines. Individuals made significantly more errors in the long interval (B; 25.91 ± 13.23%) compared to the short interval (9.68 ± 6.54%). Error bars represent standard errors of the mean.
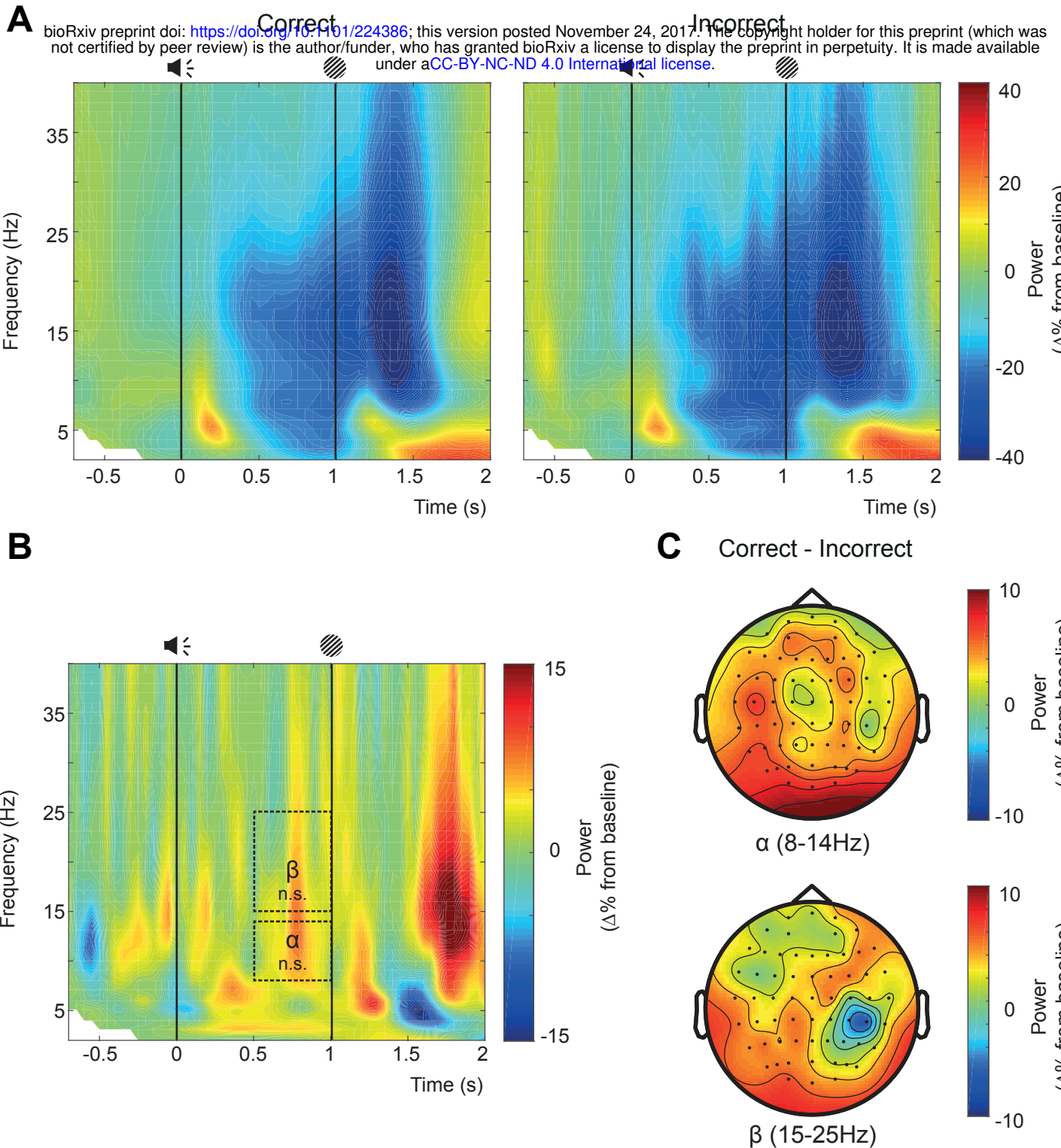
Figure 3. TFR for the short interval. The percentage change from baseline is plotted for the different frequency bands over time averaged across all electrodes, with a baseline interval from -700 to -200 ms, tone onset at t = 0 s followed by visual stimulus presentation at t = 1.0 s. Correctly perceived short intervals are visible on the left and trials incorrectly perceived as long are visible on the right (A). The difference plot shows more power for trials correctly perceived as short than trials incorrectly perceived as long (B). There were no significant differences observed in the alpha or beta band. The topography of the average activity over the time window of interest is plotted in C (correct – incorrect trials).
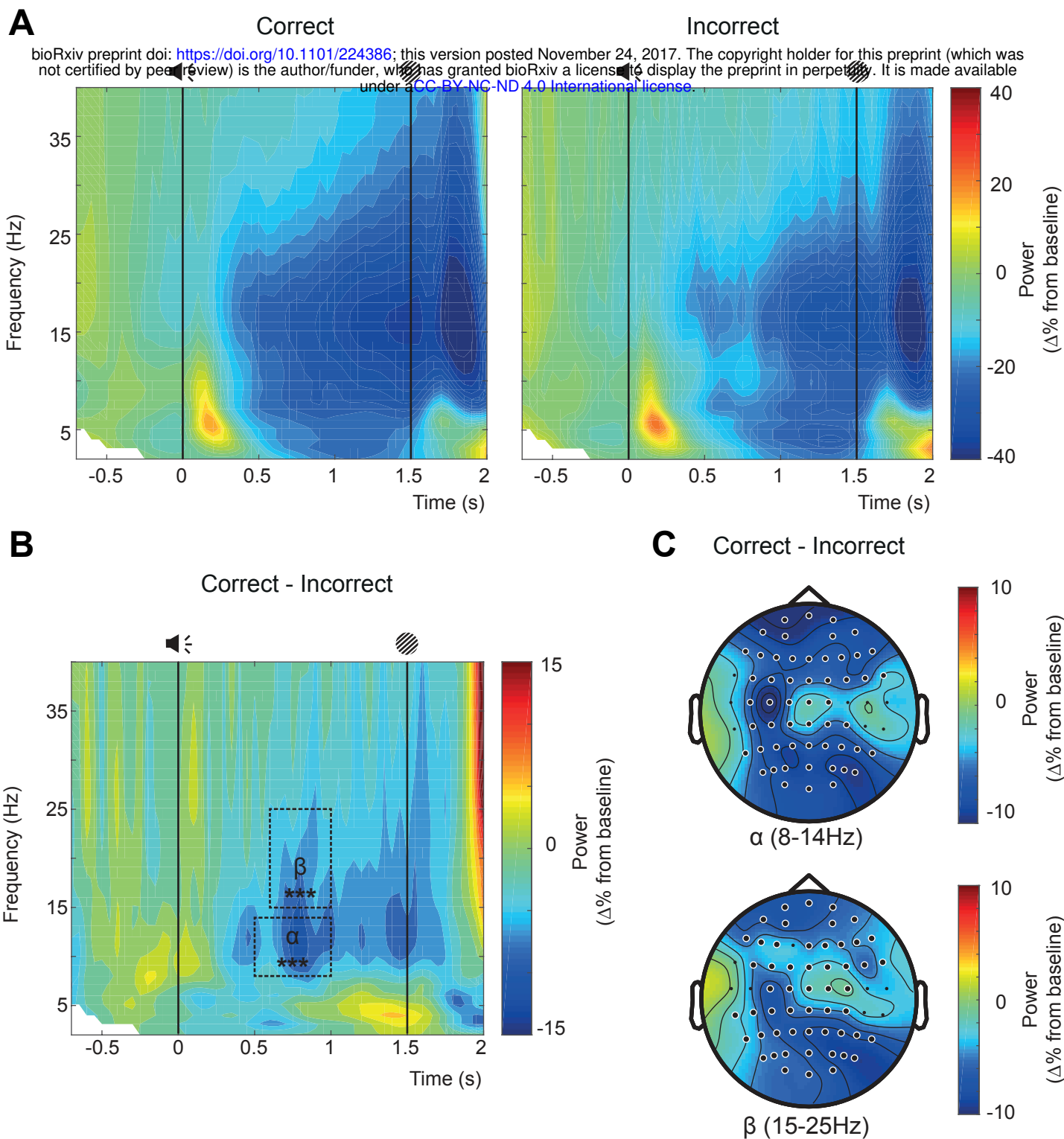
Figure 4. TFR and topographical distribution for the long interval. Same as in Fig. 3A but now with visual stimulus presentation at t = 1.5 s. The difference between correct (left in A) and incorrect (right in A) trial types is visualized in B, where power was lower for correct trials. Significant differences between correct and incorrect responses were observed in the alpha and beta bands. The topographical plots show correct-incorrect responses (C). Black circles with white edges represent electrodes showing significant modulation at any one time point, corrected for multiple comparisons using cluster randomization routine (Maris and Oostenveld, 2007).
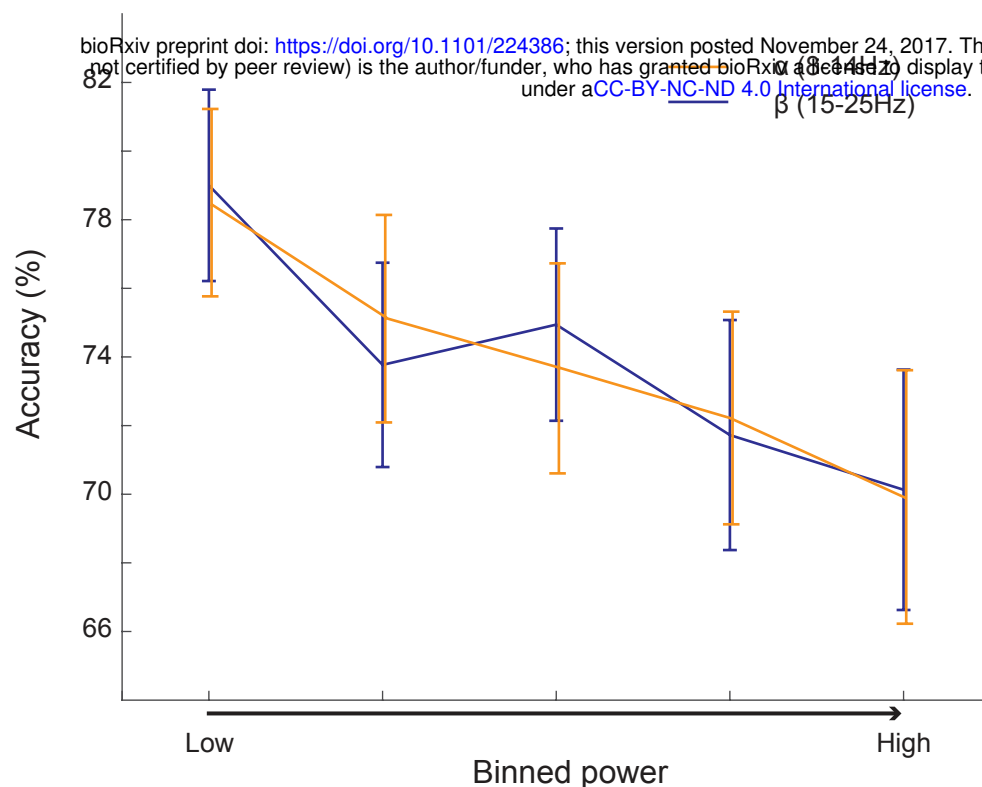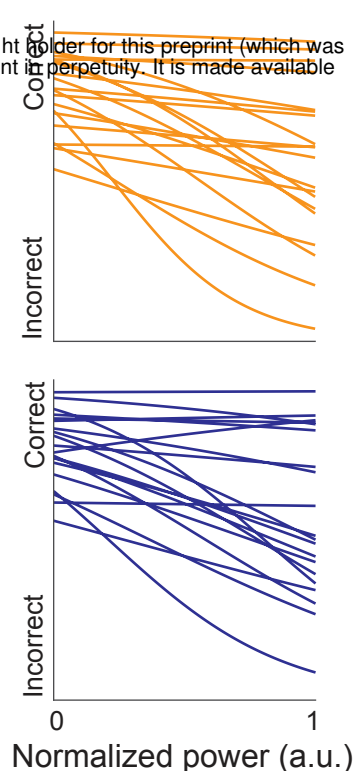
Figure 5. Accuracy as a function of power. Alpha and beta power from the clusters displayed in Figure 4C significantly predicted responses. This relationship is visualized here by plotting accuracy as a function of binned z-scored alpha and beta power, where each bin has the same amount of trials within a participant (A). As alpha and beta power increase, the accuracy decreases. Error bars represent standard error of the mean. The logistic regression lines for normalized power are shown in B (alpha on the top and beta on the bottom). Statistics reported in the text were performed on non-normalized power values to make sure that our normalization procedure did not drive the effect.